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Ontogenetic State of a Juvenile Polycotylid Plesiosaur (Sauropterygia: Plesiosauria) and its Implications for Plesiosaur Growth

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ONTOGENETIC STATE OF A JUVENILE POLYCOTYLID PLESIOSAUR (SAUROPTERYGIA: PLESIOSAURIA) AND ITS IMPLICATIONS FOR PLESIOSAUR GROWTH

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Abstract

ONTOGENETIC STATE OF A JUVENILE POLYCOTYLID PLESIOSAUR (SAUROPTERYGIA: PLESIOSAURIA) AND ITS IMPLICATIONS FOR PLESIOSAUR GROWTH

By Christina J. Byrd

Understanding ontogenetic variation in plesiosaurs from the family Polycotylidae can provide insight into the evolutionary history of this group of extinct short-necked marine reptiles from the Cretaceous period. In this study, I analyzed a juvenile polycotylid plesiosaur from the University of Nebraska State Museum (UNSM 55810). UNSM 55810 came from the Pierre Shale (99-65 Ma) of Nebraska and possesses skeletal elements that include a partial skull, nearly complete pectoral and pelvic girdles, and an assortment of paddle elements. Based on several cranial characteristics, this specimen is probably referable to the genus *Dolichorhynchops*. Previous qualitative studies have included UNSM 55810 but a formal description has not yet been done. To understand the ontogenetic variations among polycotylids, I collected metric measurements of UNSM 55810 and compared them among several related plesiosaurs. The greatest amount of change occurred in the girdle elements, particularly along the anterior and posterior edges. In contrast, the clavicles exhibit relative conservatism throughout ontogeny. This may be due to their dermal origin versus the endochondral origin of the other girdle elements. The juvenile girdle elements lack ossification along their margins, which suggests that cartilage may have been present in order to provide support at the time of birth. Changes in girdle morphology during polycotylid development resemble the evolutionary girdle morphology that occurred in earlier sauropterygians, suggesting that polycotylid ontogeny recapitulates sauropterygian phylogeny. Understanding the morphological changes during polycotylid ontogeny will enhance information for improved identification of subadult specimens. In addition, it provides insight to the evolutionary and developmental history of plesiosaur ontogeny and evolution.

Chapter 1. Introduction

Plesiosauria is an order of extinct marine reptiles that existed throughout the Jurassic and went extinct at the Cretaceous mass extinction (approximately 200 – 65.5 million years ago; Brown, 1981; Benson et al., 2012). The clade is composed of tetrapods that are secondarily adapted to an aquatic lifestyle, and are characterized by a rigid trunk and four hydrofoil-shaped flippers (Carroll and Gaskill, 1985; Wiffen et al., 1995; Caldwell, 1997). During the transition from land to sea, the fossil record preserves a gradual evolution from nothosaur-grade sauropterygians (basal clade to plesiosaurs; Sato et al., 2010) to the derived, fully aquatic plesiosaurs. One such transitional change is from axial propulsion and drag-based limbs to appendicular-dominated propulsion with lift-based limbs (Storrs, 1993; Caldwell, 1997; O'Keefe and Carrano, 2005; Sato et al., 2010). Other transition specializations include increased rigidity of the limbs, increased number of phalanges (hyperphalangy), interlocking phalanges, and modification of the pectoral and pelvic girdles in order to increase thoracic rigidity (Benson et al., 2012).

Studying ontogenetic sequences of plesiosaurs allows analysis of aspects of organismal biology that are not typically recorded in the fossil record. Understanding the ontogeny of plesiosaurs can be used to gain insight into their reproductive and life histories, such as the possibility of social structure and maternal care (O'Keefe and Chiappe, 2011). Here I propose to study the ontogenetic variation of plesiosaur bones to gain fresh insight into their reproductive biology, as well as evolutionary history of the skeletal elements.

Sauropterygia Phylogenetic History

Plesiosaurs were once occupants of the Western Interior Seaway during the Jurassic and Cretaceous, and part of a larger clade called Sauropterygia Owen, 1860 (Storrs, 1991, 1993; Bakker, 1993; Rieppel, 2000). Sauropterygians make up a monophyletic clade of carnivorous diapsid reptiles that originated around the Early to Middle Triassic and persisted for the majority of the Mesozoic era (Andrews, 1910; Romer, 1956; Rieppel, 2000; Cheng et al., 2004). The superorder Sauropterygia can be divided into two groups: stem-group sauropterygians and crown-group taxa (Rieppel, 2000). The stem-group sauropterygians originated during the Triassic and include the taxa basal to Plesiosauria, such as Placodontoidea, Pachypleurosauria, Nothosauroidea, and Pistosauroidea (Fig. 1.1; Rieppel, 1994, 2000). The crown-group taxa, the taxa that make up the order Plesiosauria de Blainville 1835, can be divided into seven families: Rhomaleosauridae, Pliosauridae, Microcleididae, Elasmosauridae, Cryptocleididae, Leptocleididae, and Polycotylidae (Fig. 1.1; Ketchum and Benson, 2010).

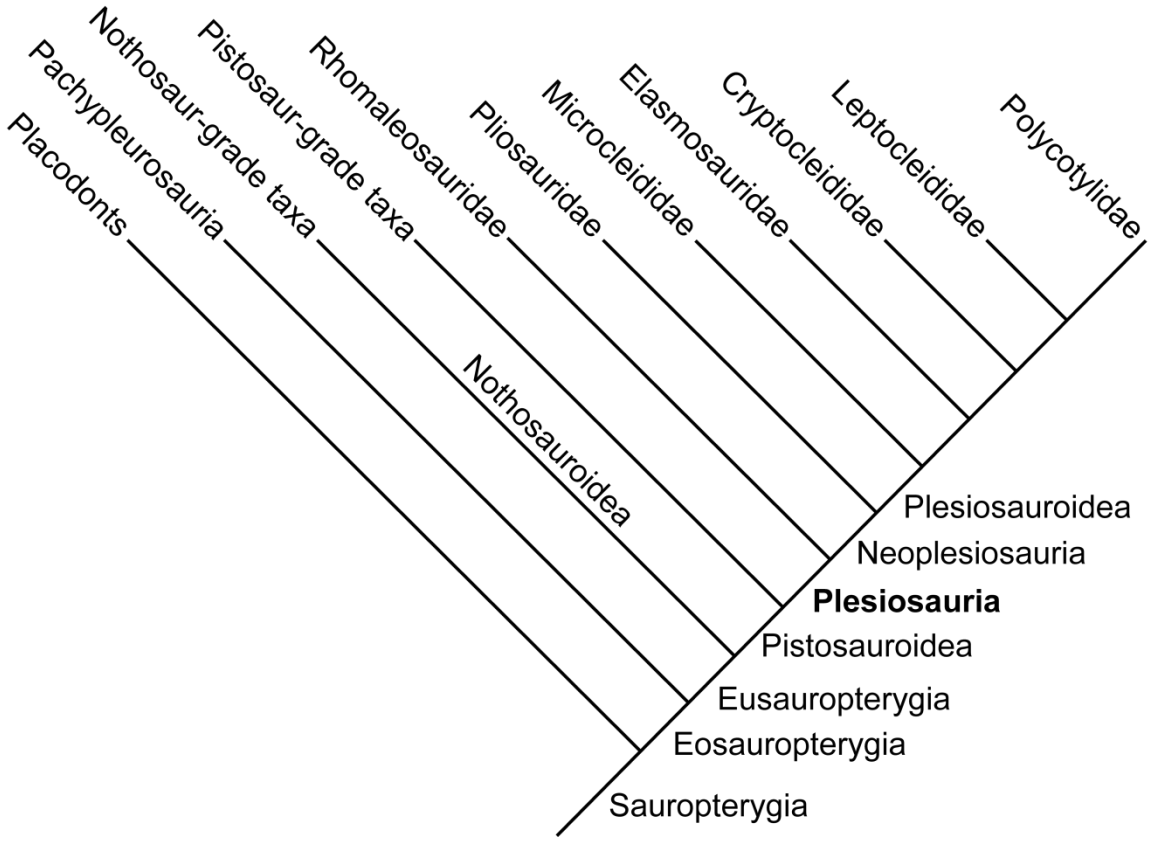

Figure 1.1. Generalized family-level phylogeny of Sauropterygia. (adapted from Rieppel, 2000, Ketchum and Benson, 2010 and Benson et al., 2012)

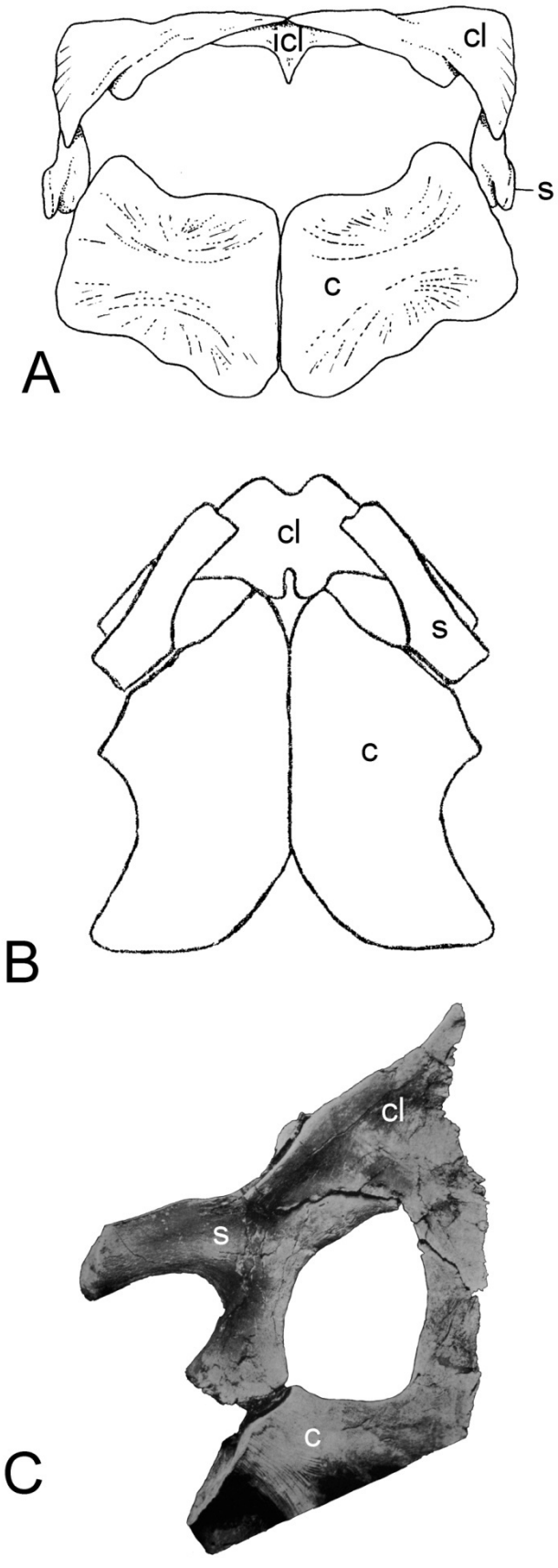

Figure 1.2. Pectoral girdle of a pistosaur-grade taxon, a basal plesiosaur, and a polycotylid. A is the visceral view of *Corosaurus alcovensis,* representing pistosaur-grade taxa (Storrs, 1991). B is the ventral view of *Plesiosaurus conybeari* representing the basal plesiosaur condition (Watson, 1924). C is the left, visceral view of *Dolichorhynchops osborni* representing the polycotylid condition (Williston, 1903). cl-clavicle, s-scapula, c-coracoid, icl-interclavicle

Pectoral Girdle Evolution

In the transition from land to sea within Sauropterygia, there was a fundamental reorganization of the pectoral girdle. The ventral aspect of the pectoral girdle in all sauropterygians is emphasized, while the lateral aspect is reduced (Storrs, 1993; Rieppel, 2000). Nothosaur-grade taxa have a reduced dorsal process on the scapula and a robust, ventrally-oriented coracoid that forms a symphysis along the posterior midline (Fig. 1.2A; Storrs, 1993; Rieppel, 2000). The anterior portion of the pectoral girdle is composed of a relatively large, robust clavicular arch, consisting of clavicles that extend from the anterior portion of the scapula to meet at the midline with an interclavicle on the ventral aspect of the clavicle (Lin and Rieppel, 1998; Rieppel, 2000; O'Keefe and Byrd, 2012). *Placodus* has a reduced coracoid condition, wherein it has an oval shape and has a notch adjacent to the scapula that represents an open coracoid foramen (Rieppel, 1994). In derived sauropterygians, the coracoid is waisted and possesses strongly concave anterior and posterior margins, a more derived condition than that found in *Placodus* (Rieppel, 1994). This strongly waisted coracoid is present in sauropterygians such as *Simosaurus*, *Nothosaurus*, and *Corosaurus* (not as strongly waisted, but still distinct; Fig. 1.3).

Plesiosaurs, such as *Plesiosaurus*, are characterized by a reduced clavicular arch and possess a scapula with an elaboration of the ventral ramus (termed 'ventral plate' by Tarlo, 1957; O'Keefe and Byrd, 2012; Fig. 1.2B). The ventral elaboration is oriented anteromedially and the anteromedial portion of the coracoids develops into anterior processes. *Westphaliasaurus*, a basal plesiosaur, has a pectoral girdle considered the most plesiomorphic condition known in plesiosaurs, possessing clavicles and an interclavicle that are relatively large elements and scapulae that exhibit significant anteromedial elaboration (Fig. 1.3; Schwermann and Sander,

2011). Also in *Westphaliasaurus*, it is clear that the waisting of the coracoid has been replaced by a hypertrophy of the anterior and posterior margins, extending the symphysis anteriorly into an anterior process that meets with the clavicular arch. The coracoid became more hypertrophied posteriorly and develops lateral horns, such as those found on *Cryptoclidus*.

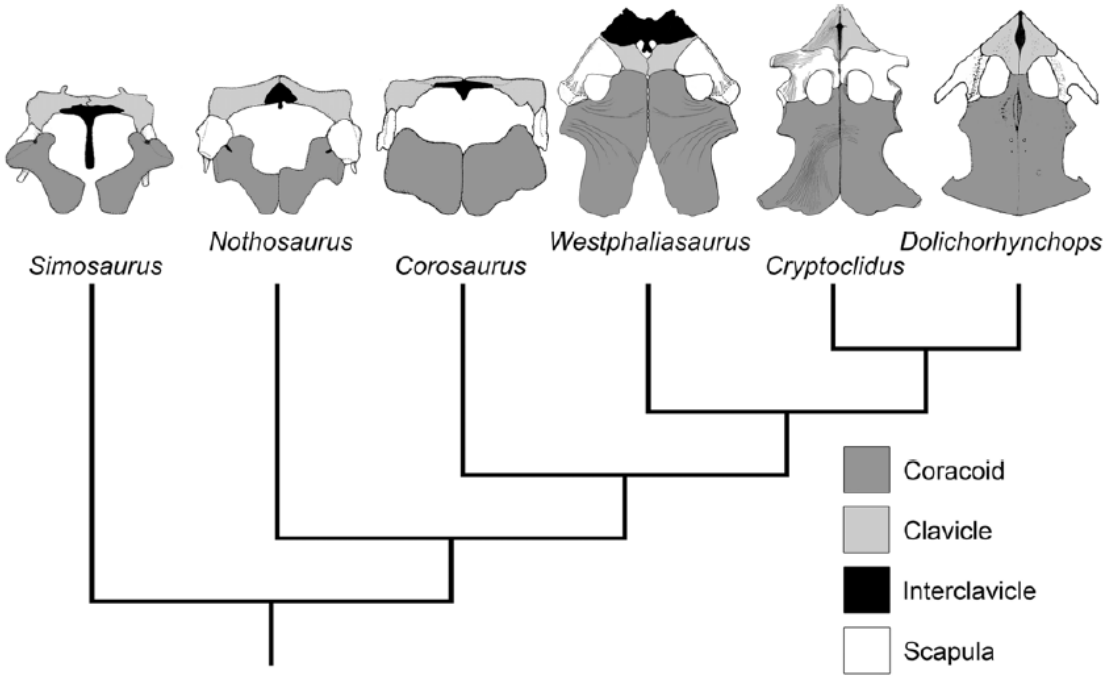

Figure 1.3. Pectoral girdle evolution within Sauropterygia (O'Keefe and Byrd, 2012). There is hypertrophy of the coracoid, which becomes more plate-like and then extends anteriorly and far posteriorly in derived plesiosaurs. The scapulae transition from a predominantly lateral element with minimal anterior elaboration in 'nothosaur-grade' taxa to an ventro-lateral element with an anterior process running anteromedially along the ventrum of derived plesiosaurs. The extent of the anterior process varies ontogenetically and phylogenetically. The dermal elements (clavicle and interclavicle) comprise the robust clavicular arch that is the most anterior aspect of the pectoral girdle in 'nothosaur-grade' taxa. In most plesiosaurs, these dermal elements are reduced and relatively unimportant. Due to the anterior process of the scapulae largely hiding the dermal elements, the girdles of *Cryptoclidus* and *Dolichorhynchops* are shown in visceral view, while the other girdles are shown in superficial view.

Polycotylid plesiosaurs have a scapular morphology similar to that of the basal plesiosaurs, such as *Plesiosaurus*, but not as extreme in elaboration as in *Cryptoclidus*. The midline symphysis is also absent in the derived plesiosaur clade Leptocleididae (early

Cretaceous) (Williston, 1906; Ketchum and Benson, 2010; Kear and Barrett, 2011). The scapulae of polycotylids have a thickened glenoid ramus with significant anteromedial elaboration of the ventral ramus and posterodorsal extension of the dorsal process (Fig. 1.2 C). The clavicles are situated on the visceral surface of the scapulae and possess a triradiate morphology with a thickened anterolateral border. The medial and posterolateral edges are thin and irregular. Along the medial edge is an embayment into which the interclavicle articulates. The coracoids of polycotylids retain the elongate, shield-like coracoid with a clearly defined coracoid symphysis, anterior process and lateral horns along the posterior portion of the bone. The exact morphology of the horns varies taxonomically.

Pelvic Girdle Evolution

The pelvic girdle demonstrates a conservative rearrangement of the pubes, ischia, and ilia compared to the pectoral girdle (Fig. 1.4). Maintained throughout all Sauropterygia is the concavity along the posterior margin of the pubes. This concavity, along with a conserved concavity along the anterior margin of the ischia, forms the thyroid fenestra in all sauropterygians (Rieppel, 1994; termed puboischiadic fenestra by Storrs, 1991 and pelvic fenestra by Sato et al., 2010). Basal sauropterygians, including *Simosaurus*, *Nothosaurus*, and *Corosaurus*, have pubes that are plate-like, meet together on the midline to form a pubic symphysis, and possess an obturator foramen just anterior to the acetabular region (Andrews, 1910; Storrs, 1991; Rieppel, 1994). The ischia are the most conserved in morphology. Among sauropterygians, they are hatchet-shaped and meet together along the midline to form an ischial symphysis (Andrews, 1910; Sato et al., 2010). The ilia of sauropterygians are primitively short,

broad, robust bones that articulate at the acetabulum (formed by the junction of the pubis and ischium) and possess facets for articulation with the sacral ribs (Rieppel, 1994).

At or near the transition to Plesiosauridae, the obturator foramen is lost and the pubes become predominantly semicircular with taxonomically variable amounts of anterolateral ornamentation (Rieppel, 1994; Rieppel, 2000; Dalla Vecchia, 2006). However, the presence of the obturator foramen appears to be taxonomically variable among pistosaurs. The pistosaurs *Corosaurus*, from the family Cymatosauridae, has the obturator foramen present, but in *Yunguisaurus*, from Pistosauridae, the foramen is absent (Fig. 1.4; Rieppel, 1994, 2000; Sato et al., 2010). With Pistosauria being a sister clade of Plesiosauria, it is probable that the absence of the obturator foramen in *Yunguisaurus* and a more derived pistosaurs *Bobosaurus* was conserved as evolution continued into the Plesiosauria (Dalla Vecchia, 2006; Benson et al., 2012). From the basal sauropterygian *Simosaurus* to the more derived nothosaur-grade sauropterygians (e.g. *Nothosaurus* and *Corosaurus*), the ilium loses the articulating facets for the sacral ribs but retains the relatively short length (Rieppel, 1994). Among the pistosaurs, these articulating facets are missing (Rieppel, 1994). Articulation of the ilium with the sacral ribs would thus be made via cartilage.

The morphological variation of the pubes among plesiosaurs occurs predominantly along the anterolateral edge. The ornamentation, or lack thereof, varies depending on taxa. Basal plesiosaurs, such as *Westphaliasaurus* and *Microcleidus*, tend to lack anterolateral ornamentation (Watson, 1909; Schwermann and Sander, 2011). The overall morphology does not vary much from the semi-circular pubes found in pistosaurs. However, polycotylids and cryptoclidids have an anterolateral horn present in addition to the semi-circular pubes (Andrews, 1910). In polycotylids, the posterior margin of the ischium extends far posteriorly, in some cases extending

to a length twice the width of the ischium. This elongation of the ischium is a trend commonly seen among pliosauromorph (short-necked) plesiosaurs regardless of clade membership (O'Keefe, 2002). At or near the node Plesiosauria, there is also a shift in the location of the ilium. In plesiosaurs, the ilium articulates solely with the ischium, and becomes elongate, slender and in some cases blade-like or curved. Among polycotylids, the morphological characteristics (e.g. blade-like and straight or rod-like and curved) of the ilium vary and become important in differentiating among polycotylid taxa (O'Keefe and Byrd, 2012).

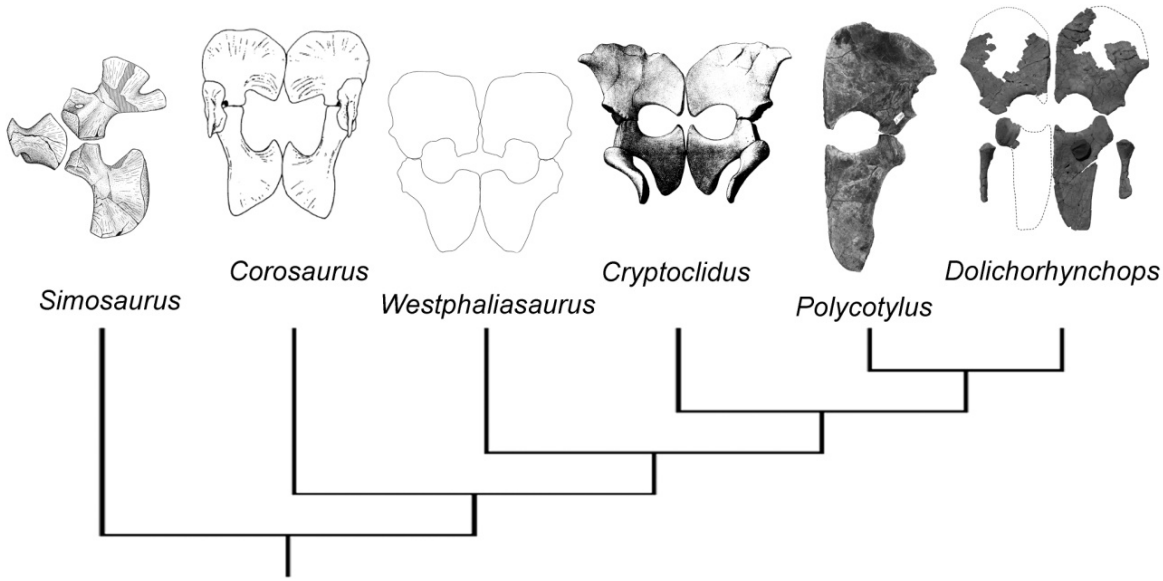

Figure 1.4. Sauropterygian pelvic girdle phylogeny. *Simosaurus* from Rieppel (1994), *Corosaurus* from Storrs (1991), *Westphaliasaurus* from Schwermann and Sander (2011), *Cryptoclidus* from Andrews (1910), *Polycotylus* (LACM 129639a), and *Dolichorhynchops* from Schmeisser McKean (2012). Early in the evolution of sauropterygians, the obturator foramen is lost (Andrews, 1910; Storrs, 1991; Rieppel, 1994). The pubes retain a relatively semicircular shape throughout phylogeny but in more derived plesiosaurs, bony elaborations form along the anterolateral border. The ischia maintain a hatchet shape, but among the polycotylids, this hatchet shape is more elongate (Andrews, 1910; Watson, 1909; Schmeisser McKean, 2012).

Specimen Classification

The primary focus of this research is on UNSM 55810, a juvenile polycotylid plesiosaur held at the University of Nebraska State Museum (UNSM), which was excavated from the Pierre Shale (99-65 Ma) of South Dakota. It is a partial skeleton possessing a partial skull, nearly complete pectoral and pelvic girdles, the left humerus, both femura and an assortment of distal paddle elements. This juvenile has not been formally described, though it has been used in other qualitative studies, such as Massare (1987), Carpenter (1996) and O'Keefe (2008). Polycotylid plesiosaurs are a part of a body type group termed pliosauromorphs (O'Keefe, 2002). Pliosauromorphs, in contrast to plesiosauromorphs, have relatively large heads, short necks, and hindlimbs that tend to be longer than their forelimbs (Rieppel, 2000; O'Keefe, 2002). O'Keefe (2002) found that the pliosauromorph body type is polyphyletic within Plesiosauria. However, there is not always a clear distinction of some clades into one of these morphs. The body types occur on a spectrum with intermediate forms, such as those found in the clade Cryptocleididae, which have an intermediate sized head and neck length (O'Keefe, 2002). Recent phylogenetic analysis by Ketchum and Benson (2010) placed Polycotylidae within Plesiosauroidea, therefore, this is the same attribution I will be following for this research.

Massare (1987) and O'Keefe (2008) suggested UNSM 55810 is referable to the genus *Dolichorhynchops*. O'Keefe (2008) described similarities between both *D. osborni* and *D. bonneri*, but noted that the juvenile was likely more closely related to *D. bonneri*. The characters O'Keefe (2008) used as diagnostic are cranial elements including: teeth with relatively low and robust crowns, laterally narrow and long lateral plates of the pterygoids, presence of an ectopterygoid that is carried on a distinct process, and evidence of the anterior palate demonstrating that the internal nares were anterior to the end of the pterygoids. However,

presence of a parasphenoid with an anterior process extending into the anterior interpterygoid vacuity supported classification within *D. osborni*. Due to the poor ossification of the skull of the juvenile, these four traits are the only diagnostic features and lead to a conservative referral of UNSM 55810 to the family level of Polycotylidae and the genus *Dolichorhynchops* (O'Keefe, 2008).

It has been suggested that postcranial characteristics are not as reliable in determining taxonomic classifications based on the possibility that they are more likely to have been affected by convergent evolution due to the ecological constraints imposed by an aquatic environment (Carpenter, 1997). However, Ketchum and Benson (2010) found that there is only a small difference between the consistency of cranial and postcranial characters used in phylogenetic analysis. Therefore, the postcranial elements of UNSM 55810 need to be taken into consideration as well. A recent study by O'Keefe and Byrd (2012) suggests that the clavicle can also be used to classify the juvenile to Polycotylidae based upon its triradiate morphology, and that the ilium supports a referral to the genus *Dolichorhynchops*.

Skeletal Allometric Growth

Numerous authors have discussed the ontogenetic development of plesiosaurs; however, confident understanding of ontogeny is limited by the availability of fossils. With ontogeny comes an understanding of the allometry of plesiosaurs. Allometry describes the differences in proportions of bones of similar function at different body sizes (Gould, 1966; Lin and Rieppel, 1998).

There is good fossil evidence of allometric growth throughout the ontogeny of the taxon *Cryptoclidus* from the Oxford Clay of London (Andrews, 1910). *Cryptoclidus* is a plesiosauroid

from the family Cryptocleididae and is a closely related taxon to Polycotylidae (O'Keefe, 2002). In addition, *Cryptoclidus* has a pectoral girdle that demonstrates morphological characteristics that resemble ancestral taxa, such as *Plesiosaurus* and *Westphaliasaurus* (Fig. 1.5; Andrews, 1910; Ketchum and Benson, 2010; Schwermann and Sander, 2011; O'Keefe and Byrd, 2012). The juvenile *Cryptoclidus* scapula (Fig. 1.5A) has a morphology that is drastically different than that of the adult. It has elongate ventral rami that extend anteromedially but do not contact at the midline, much like basal plesiosaurs. As ontogeny progress, the ventral rami of the scapulae elongate further and eventually contact to form a symphysis at the midline in the adult (Fig. 1.5B-C). After contact is made, growth continues posteriorly along the midline until contact is made with the anterior process of the coracoid (Fig. 1.5C).

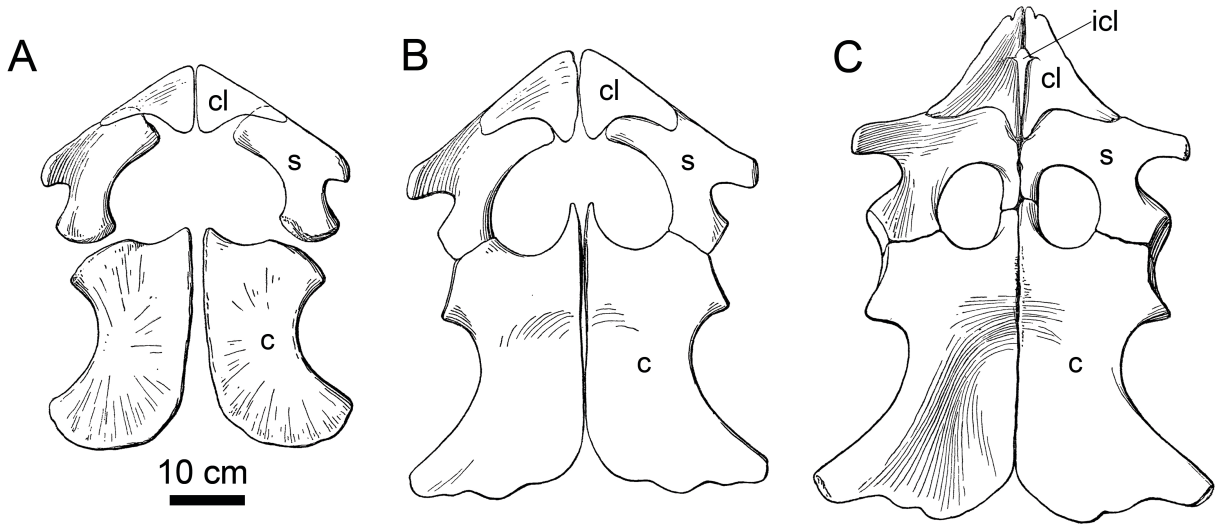

Figure 1.5. *Cryptoclidus oxoniensis* pectoral girdle ontogenetic series: (A) juvenile, (B) subadult, and (C) adult (Andrews, 1910; Schwermann and Sander, 2011; O'Keefe and Byrd, 2012). The scapulae of the juvenile and subadult *Cryptoclidus* have a morphology that resembles that of basal plesiosaurs such as *Plesiosaurus* and *Westphaliasaurus.* As *Cryptoclidus* ontogeny progresses, the ventral rami meet at the midline and growth continues posteriorly, forming a medial symphysis of the scapulae and contact with the coracoids. Abbreviations: c-coracoid, cl-clavicle, icl-interclavicle, s-scapula

The pelvic girdle of *Cryptoclidus* has a much more conserved ontogeny (Fig. 1.6). The pubes show the greatest variation in morphology throughout ontogeny with the elaboration of the anterolateral margin. The pubes closely resemble the morphologies of the basal plesiosaurs *Westphaliasaurus* and *Microcleidus* (Watson, 1909; Andrews, 1910; Schwermann and Sander, 2011). The ischia and ilia of the juvenile do not differ much from that found in adult *Cryptoclidus* (Fig. 1.6A). In addition, the morphology of the pubes and ischia closely resemble that of basal sauropterygians, such as *Corosaurus* and *Bobosaurus*, and basal plesiosaurs, such as *Westphaliasaurus* and *Microcleidus* (Fig. 1.6A; Watson, 1909; Andrews, 1910; Storrs, 1991; Dalla Vecchia, 2006; Schwermann and Sander, 2011). In the adult *Cryptoclidus*, the anterolateral margins of the pubes have developed a horn-like ornamentation that points laterally (Fig. 1.6B).

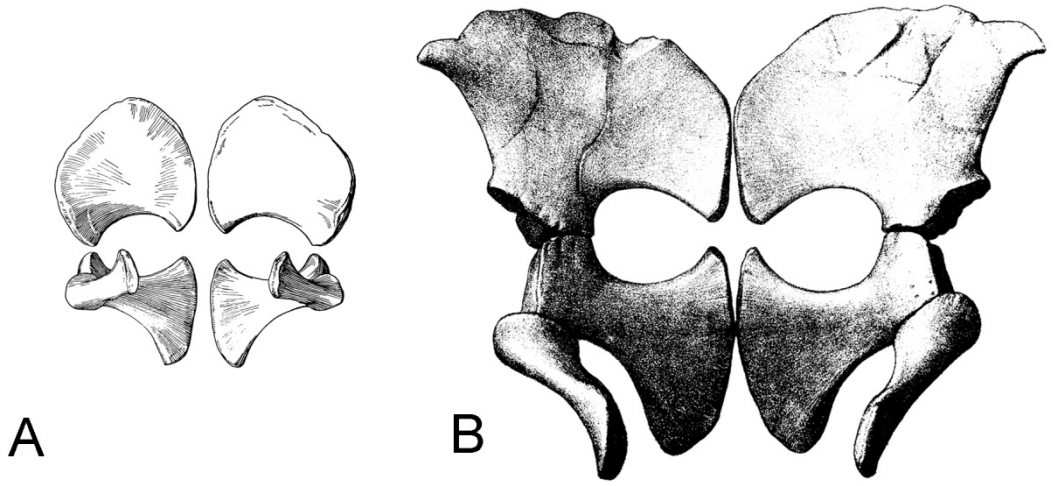

Figure 1.6. Ontogenetic series of *Cryptoclidus oxoniensis* pelvic girdle: A) juvenile and B) adult (Andrews, 1910). Note the amount of anterolateral elaboration on the pubes during ontogeny and the dearth of shape change in the ischia and the ilia.

O'Keefe and Chiappe (2011) conducted a study on an adult polycotylid plesiosaur, from the Natural History Museum of Los Angeles County (LACM), that was preserved with a fetal plesiosaur of the same species inside it. The adult and fetal plesiosaurs, LACM 129639a and LACM 129639b, were discovered on Bonner Ranch in Logan County, Kansas from the Sharon

Springs Member of the Pierre Shale (Campanian; O'Keefe and Chiappe, 2011), the same formation from which the specimen of this study was found. LACM 129639a, hereon referred to as the adult, has several characteristics that refer it to *Polycotylus latipinnis* (O'Keefe and Chiappe, 2011). In order to compare the sizes of the adult and fetal plesiosaurs, O'Keefe and Chiappe (2011) calculated the geometric mean, an average of the product of multiple morphological variables, as a size index. The elements included in calculating the mean were: scapula, coracoid, pubis, ischium, humerus and femur (O'Keefe and Chiappe, 2011).

Their work provides information about possible life history aspects of plesiosaurs, such as viviparity and small brood size. This specimen, LACM 129639, although from a different genus, will provide a basis for determining the ontogenetic stage of UNSM 55810. O'Keefe and Byrd (2012) showed that what O'Keefe and Chiappe (2011) identified as a humerus in the fetal material is in fact a scapula. This correction led to the reevaluation of all the skeletal elements of the fetus, and subsequently, other identifications were corrected. Due to these misidentifications, recent research was conducted on the pectoral girdle of the fetus, in comparison to the adult and the juvenile polycotylids (O'Keefe and Byrd, 2012). The results of that study are included with the description and analysis of UNSM 55810 within this thesis (Ch. 2).

Cartilage development and ossification

Cartilage, a relatively soft and flexible translucent substance containing fibrous material, is present in reptiles and of embryological importance (Romer, 1956). Any skeletal structure that is present deep in the body appears first as cartilage (Romer, 1956). This cartilaginous precursor prior to full bone development is critical in the early stages of ontogeny. In order for skeletal elements to expand and grow from the tiny size in embryos to the adult form, growth needs to

occur without continual disturbance of articulations with other elements (skeletal, muscular, and other external relations; Romer, 1956).

Perichondral and endochondral ossification in limb bones

Throughout development, a cartilaginous precursor ossifies via endochondral ossification except for those bones originating in the dermis (Romer, 1956; Weatherbee and Niswander, 2007; Amizuka et al., 2012). In the long bones of reptiles, early stages of ossification involve the deposition of perichondral bone forming the periosteum around the center of the primordial cartilage (Romer, 1956; Caldwell, 1997). Perichondral and endochondral bone formation requires the presence of cartilage containing perichondral and endochondral chondrocytes (cartilage producing cells) prior to osseous deposition (Romer, 1956; Caldwell, 1997). The cartilage is not replaced immediately. Perichondral ossification tends to occur prior to the initiation of endochondral ossification (Rieppel, 1992; Caldwell, 1997). As the long bone develops, layer upon layer of perichondral bone is deposited as a dense matrix around the cartilage, creating a sheath (Fig. 1.7; Caldwell, 1997; Liebe and Hurum, 2012). Eventually the cartilage is resorbed and endochondral bone replaces it in the form of a spongy matrix sheathed by the perichondral bone (Romer, 1956; Caldwell, 1997; Farnum, 2007). In sections of the long bone that were smaller before replacement, the resorbed cartilage would produce a marrow cavity (Romer, 1956).

In plesiosaurs, the growth of perichondral and endochondral bone is distinct and distinguishable in young bones (Moodie, 1916; Liebe and Hurum, 2012). These bones illustrate bone deposition that occurred in multiple directions, resulting in a cleavage plane between the perichondral and endochondral bone layers and an overall different bone structure (Moodie,

1916; Liebe and Hurum, 2012). Plesiosaur stylopod elements (termed propodials) start with two cartilaginous cone precursors within a sheath of periosteal bone (also termed cortex; Fig. 1.7; Liebe and Hurum, 2012). The apices of both cones are pointed toward the center of the propodial, but do not meet and are separated probably by a small medullary cavity (an open cavity in the bone; Fig. 1.7; Liebe and Hurum, 2012). During development, these cartilaginous cones ossify and become endochondral bone (Liebe and Hurum, 2012). This pattern of having two endochondral cones within a sheath of perichondral bone has been described in mammals such as *Trichchus latiostris* (manatee) and *Delphinus delphis* (dolphin) and reptiles including *Dermochelys coriacea* (leatherback turtle), sauropterygians (*Pachypleurosaurus* and *Placodus*), and observed in plesiosaurs (Liebe and Hurum, 2012). Plesiosaurs share these cartilage cones, and the lack of a large medullary cavity, with other aquatic taxa, such as cetaceans (e.g. whales and dolphins) and large marine turtles (Liebe and Hurum, 2012). In Liebe and Hurum's (2012) study of plesiosaur propodials, they found that juvenile specimens had a small medullary cavity, subadults had little to no medullary cavity, and it seems to disappear completely in adults. Being secondarily adapted to an aquatic environment, plesiosaurs underwent a transition in bone histology through out ontogeny. This alteration of the bone occurred as mass increased into adulthood and influenced the animal's buoyancy in water (Liebe and Hurum, 2012). This buoyancy could suppress the skeleton's weight-bearing role and this in turn can alter the histology of the bones (Liebe and Hurum, 2012).

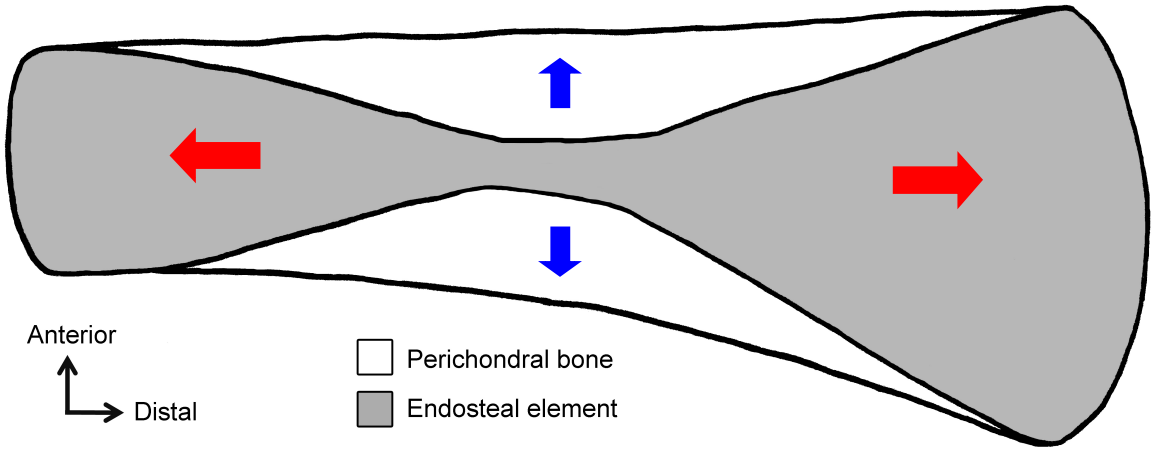

Figure 1.7. Endochondral and perichondral ossification of juvenile plesiosaur propodials. General pattern adopted from Liebe and Hurum (2012). The red arrows illustrate the direction of cartilage growth and ossification of the endosteal element as it becomes endochondral bone. The bone arrows indicate the general direction of growth as the perichondral bone layers upon and around the endochondral bone.

Reduction and loss of the medullary cavity in response to an aquatic environment is thought to strengthen the limb bones for resistance to bending during swimming (Liebe and Hurum, 2012). With this alteration of the medullary cavity, there are also changes in the overall mass of the bones, possibly due to the speed at which a particular animal swims (Liebe and Hurum, 2012). Animals that live close to the shore and do not rely upon fast swimming tend to have a general increase in skeletal mass. However, animals that live in the open sea and use fast and sustained swimming tend to have lighter bones, while still lacking the medullary cavity (Liebe and Hurum, 2012).

The periosteal sheath, or cortex, that surrounds the cones does not cover the entire length of the propodial in the earliest stages of development, but instead bridges the gap between the apices of the cones surrounding the medullary cavity (Farnum, 2007; Liebe and Hurum, 2012). As development continues, layers of periosteum are added and eventually wrap around the

majority of the bone, except where articular cartilage remains at joints. Since the perichondral bone does not cover the entire bone initially, once the bone is covered, it is not surprising that the bone would have areas of differing perichondral thickness (Liebe and Hurum, 2012). This perichondral bone is typically more compact than the endochondral cones (Liebe and Hurum, 2012).

Perichondral and endochondral ossification in non-long bones

Endochondral elements occur primarily in the postcranial skeleton, such as the scapulae and coracoids of the pectoral girdle, pelvic girdle elements and limb bones, and certain bones of the cranium (Romer, 1956). Cartilage can persist well into adulthood but primarily in regions where flexibility is desired (Romer, 1956). Peripheral cartilage is common in regions of the scapulae and coracoids of many reptiles, as well as along the ventral margins of the pubes and ischia in reptiles in general (Romer, 1956). In marine reptiles, it has been observed that cartilage is frequently retained in the limb and girdle skeletons and that incomplete ossification of these elements in extinct taxa implies a marine lifestyle (Romer, 1956).

In this study, I looked at the propodials of a juvenile plesiosaur, but I emphasize the pectoral and pelvic girdle elements. The girdle elements are interesting from a bone ossification viewpoint because of a peculiar feature on several of the elements that allude to the ossification pattern of axial skeletal elements in plesiosaurs at early ontogenetic stages. Having a strong understanding of cartilage formation and ossification is important because cartilage usually does not preserve during the process of fossilization. Therefore, by understanding the patterns in a variety of other taxa, I can infer probable patterns in my study specimen.

Dermal ossification

Dermal bones are formed directly from the dense connective tissue residing in the dermis without the need of a cartilaginous precursor (Romer, 1956). In reptiles, dermal bone formation occurs primarily in the cranium and includes postcranial bones such as the interclavicle and clavicle (Romer, 1956; Rieppel, 1993). Ossification begins by the condensation of cells programmed for bone development (Witten and Huysseune, 2007). As these cells congregate, they differentiate into osteoblasts, cells that later become bone (Witten and Huysseune, 2007). An initial secretion of unmineralized matrix forms around the osteoblasts, which is then followed by mineralization of the matrix, ultimately forming the ossified bone (Witten and Huysseune, 2007).

Order of ossification

In general, for reptiles, the dermal elements are the first to begin ossification (Rieppel, 1993). Following the dermal elements are the limb bones. Primarily, it is the areas associated with movement and subjected to stresses that begin to ossify first, followed by subsequent application and changes of mechanical stress on the individual elements (Witten and Huysseune, 2007). After these elements have begun to ossify, the order of ossification continues from the most anterior elements, then progressing posteriorly (Rieppel, 1993). Pectoral girdle ossification starts with the interclavicle and clavicles (dermal elements), followed by the scapulae and then the coracoids (Rieppel, 1993). The pelvic girdle ossification pattern does show some variability among taxa. In lepidosaurs, such as *Lacerta*, ossification of the pelvic girdle starts with the ilium, followed by the pubis and ischium (Rieppel, 1993). In archosaurs, such as the alligator,

ossification starts again with the ilium but the following element is the ischium, then the pubis (Rieppel, 1993).

Statement of the Problem

To date, only two subadult specimens from the family Polycotylidae have been found. Due to the rarity of such specimens, the ontogeny of Polycotylidae is not well understood. Therefore, a proper description of the juvenile specimen UNSM 55810 needs to be produced in order to observe differences in the bone morphologies as they relate to adult polycotylid specimens. Also, quantifying these differences will enable a more accurate analysis of the shape data. Comparisons among the early stage and adult stage specimens will provide information on allometric growth differences among various skeletal elements.

Geologic Background

UNSM 55810 was excavated from the Sharon Springs Member (Campanian) of the Pierre Shale Formation in the Wallace Ranch locality of Fall River County, South Dakota (O'Keefe, 2008; Everhart, 2009). The Sharon Springs Member is a fissile black shale containing organic clays, concretions, and numerous bentonites (Martin et al., 2007). Martin et al. (2007) heavily reviewed and revised the Pierre Shale formation and suggested an elevation in the lithostratigraphic rank of the Pierre Shale and its associated members (O'Keefe and Byrd, 2012). This elevation of rank would make the Pierre Shale a group and its associated members would become formations (Martin et al., 2007). Martin et al. (2007) also suggested that the Sharon Springs Member, if elevated to formation rank, contains three members (Burning Brule Member,

Boyer Bay Member, and Nicholas Creek Member). Martin's scheme has not been widely followed; therefore, for the purpose of this thesis, the traditional stratigraphy is used.

Institution Abbreviations - KUVP, Kansas University Museum of Natural History, Lawrence, KS USA; **FHSM**, Fort Hays Sternberg Museum of Natural History, **LACM**, Natural History Museum of Los Angeles County, Los Angeles, CA USA; **UNSM**, University of Nebraska State Museum, Lincoln, NE USA; **YPM**, Yale Peabody Museum, New Haven, CT, USA.

Chapter 2

Materials

The elements of UNSM 55810 used in this study include the right clavicle, the scapulae, coracoids, pubes, ischia, and the left ilium (Fig. 2.1).

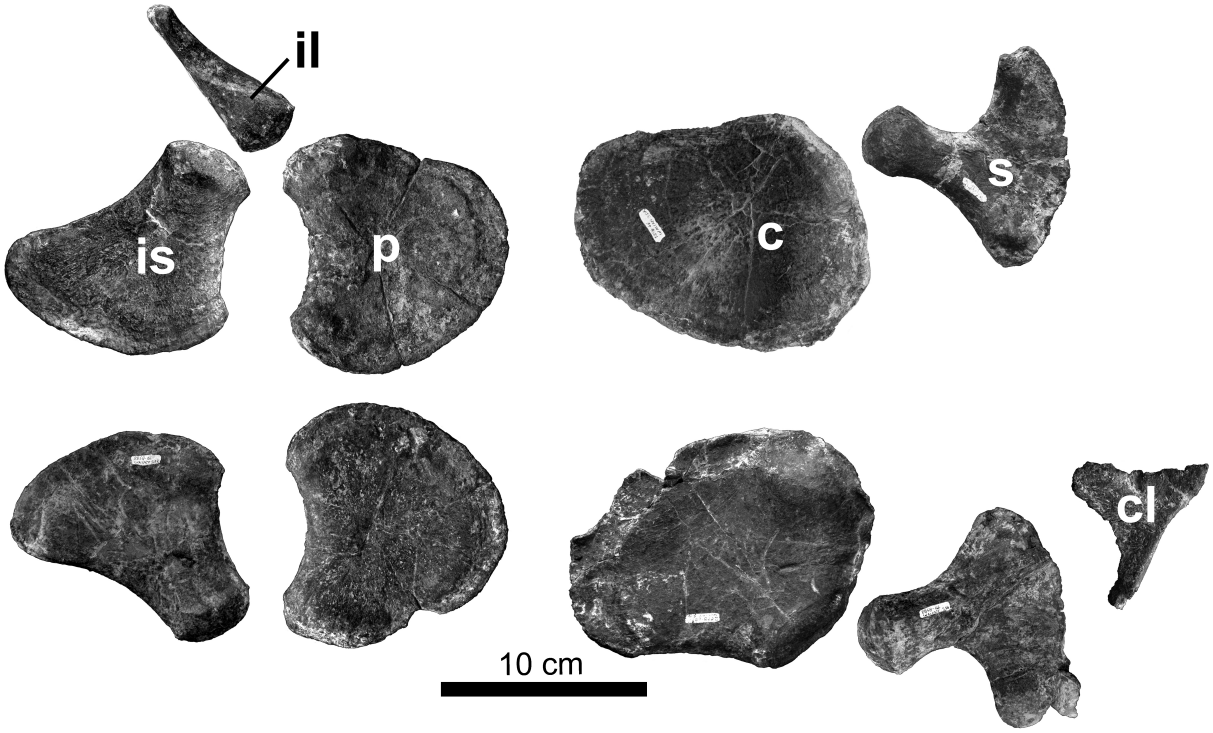

Figure 2.1. Visceral view of pectoral and pelvic girdles of UNSM 55810. c – coracoid, cl – clavicle, il – ilium, is – ischium, p – pubis, s – scapula

Methods

The morphology of each skeletal element of UNSM 55810 was compared with reference specimens including, but not limited to, LACM 129639a and b and KUVP 1300 (Table 2.1). In addition, the morphology of the juvenile was compared to ancestral sauropterygians such as nothosaur-grade taxa, pistosaur-grade taxa and basal plesiosaurs from the literature. To

understand the changes occurring during ontogeny, metric measurements were taken using calipers in millimeters (mm) to an error of 0.5 and analyzed using bivariate regression (Table 2.2).

Length of the scapula was measured using calipers from the anterior-most point of the anterior ramus to the posterior-most point of the glenoid process, parallel to the sagittal plane. Width was measured from the most medial point of the ventral ramus to the most distal point of the dorsal process, perpendicular to the sagittal plane. The lengths of the coracoids were measured from the anterior of the glenoid prominence to the posterior edge parallel to the sagittal plane. They were also measured for width from the posterior of the glenoid prominence to the medial edge perpendicular to the sagittal plane. The pubes were measured from the anterior of the acetabular process to the medial edge perpendicular to the sagittal plane for width and from the posterior of the acetabular process to the anterior edge parallel to the sagittal plane for length. The ischia were measured from the anterior of the acetabular process to the posterior end parallel to the sagittal plane for length and from the posterior of the acetabular process to the medial edge perpendicular to the sagittal plane for width.

Results: Pectoral Girdle

Clavicles

The clavicle of the juvenile (UNSM 55810) shares several morphological characteristics with the clavicles of the fetus (LACM 129639b) and KUVP 1300 (adult *D. osborni*; Fig. 2.2A-C). The clavicles possess a triradiate shape and they share a thickened anterolateral edge. A deep embayment is present on the posterolateral edge with a shallow fossa and thin, irregular edge present on the midline. When the clavicles are paired together, the midline concavities

form a foramen into which the interclavicle articulates. In addition, they share thin, irregular edges along the posterolateral border and a shallow depression along the posterolateral concavity in visceral view, along which the anterior ramus of the scapula would articulate on the ventral side of the clavicle. The clavicle from UNSM 55810 has an anterior-posterior length of 65.5 mm, anterior-lateral length of 82 mm, and a lateral-posterior length of 69.5 mm.

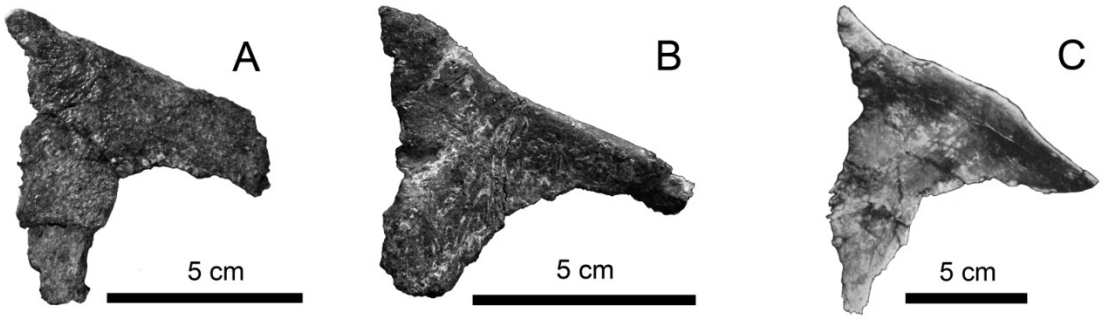

Figure 2.2. Polycotylid clavicle ontogeny. A) LACM 129639b (fetus), left ventral clavicle of B) UNSM 55810 (juvenile), and flipped right ventral clavicle of C) KUVP 1300 (adult *D. osborni*). All three clavicles share the triradiate morphology as well as a small concavity along the midline, a deep posterolateral concavity, and a thickened anterolateral edge (O'Keefe and Byrd, 2012). The clavicles of these derived plesiosaurs are reduced compared to the robust clavicular arch of basal sauropterygians.

Scapulae

The juvenile's scapulae lack elaboration of the ventral ramus and the dorsal process is poorly developed, with little ossification along the anterior edge (Fig. 2.3B). The dorsal process has a thickened posterior edge and extends posterolaterally. The dorsal process has an anterior edge that is confluent with that of the ventral ramus. Along this anterior edge, the bone is thin and irregular. Posteriorly from the anterior edge, there is a thickening of the bone that is better developed. This difference in ossification may represent the point to which the periosteal bone grew and the extension of calcified cartilage or endochondral bone (from here on termed endosteal element). Where the extended endosteal element meets the perichondral bone, there is

a lip or ridge indicating the transition. The transition can be seen on both the visceral and ventral sides of the scapulae (Fig. 2.4 and 2.5). The scapular ridge, which extends from the posterior end of the glenoid process anteromedially along the medial edge of the ventral ramus, is well developed along the border of the ventral ramus, and the glenoid process is identical to the condition found in the embryo. The glenoid process is the most robust and well-developed portion of the scapula. It extends posteriorly and terminates as a bulbous mass bearing the anterior facet of the glenoid fossa. Scapulae lengths are 101.5 mm for the right and 104.5 mm for the left. Widths of the scapulae are 107 mm for the right and 105.5 mm for the left. The juvenile scapula closely resembles that of the fetus (LACM 129639b), more so than it does the adult scapula (LACM 129639a; Fig. 2.3).

The scapula of the fetus (LACM 129639b, Fig. 2.3A) lacks elongation of the ventral ramus and the dorsal process is slightly shorter than the juvenile. The scapular crest is poorly developed, but there is thickened bone present on the ventral surface of the scapula. Like the juvenile scapula, the fetal scapula possesses a transitional lip representing the endosteal element and perichondral bone on the visceral and ventral sides (Fig. 2.6 and 2.7). The scapulae of LACM 129639b have the lip present but the right lip is not as well preserved as the left; therefore, the lip is minimal or not present. The left scapula does indicate cartilage with a lip pattern that closely resembles that in UNSM 55810. The lengths of the scapulae measure 95 mm for the right and 98 mm for the left. The widths of the scapulae are 84 mm for the right and 88 mm for the left.

The scapula of the adult (LACM 129639a; Fig. 2.3C) has an elongate ventral ramus, much like the morphology of *D. osborni* and other specimens from Polycotylidae, ancestral Microcleididae and Leptocleididae. The ventral ramus extends anteromedially and the dorsal

process extends posterolaterally. As the dorsal process extends posterolaterally, it tapers and forms a blunt-ended process. Unlike the condition found in *D. osborni*, the dorsal process of the adult scapula lacks a bend at midshaft, thereby supporting the classification of the adult to *Polycotylus*. The length of the adult scapula is 330 mm and the width is 413.8 mm.

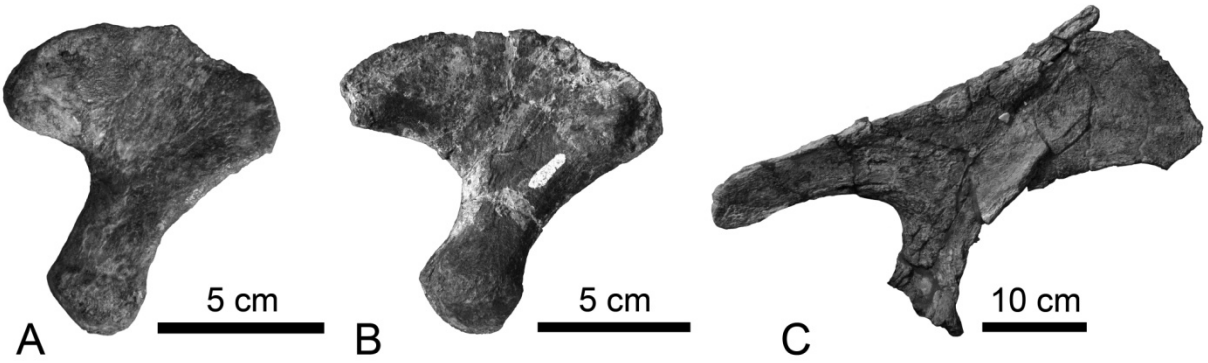

Figure 2.3. Scapula ontogeny of polycotylids. Visceral view of the left scapulae of A) LACM 129639b (fetus), B) UNSM 55810 (juvenile), and C) LACM 129639a (adult). Note the lack of elongation along the anterior ramus and the proportionally shorter dorsal process of the fetus and juvenile as compared to the adult (O'Keefe and Byrd, 2012).

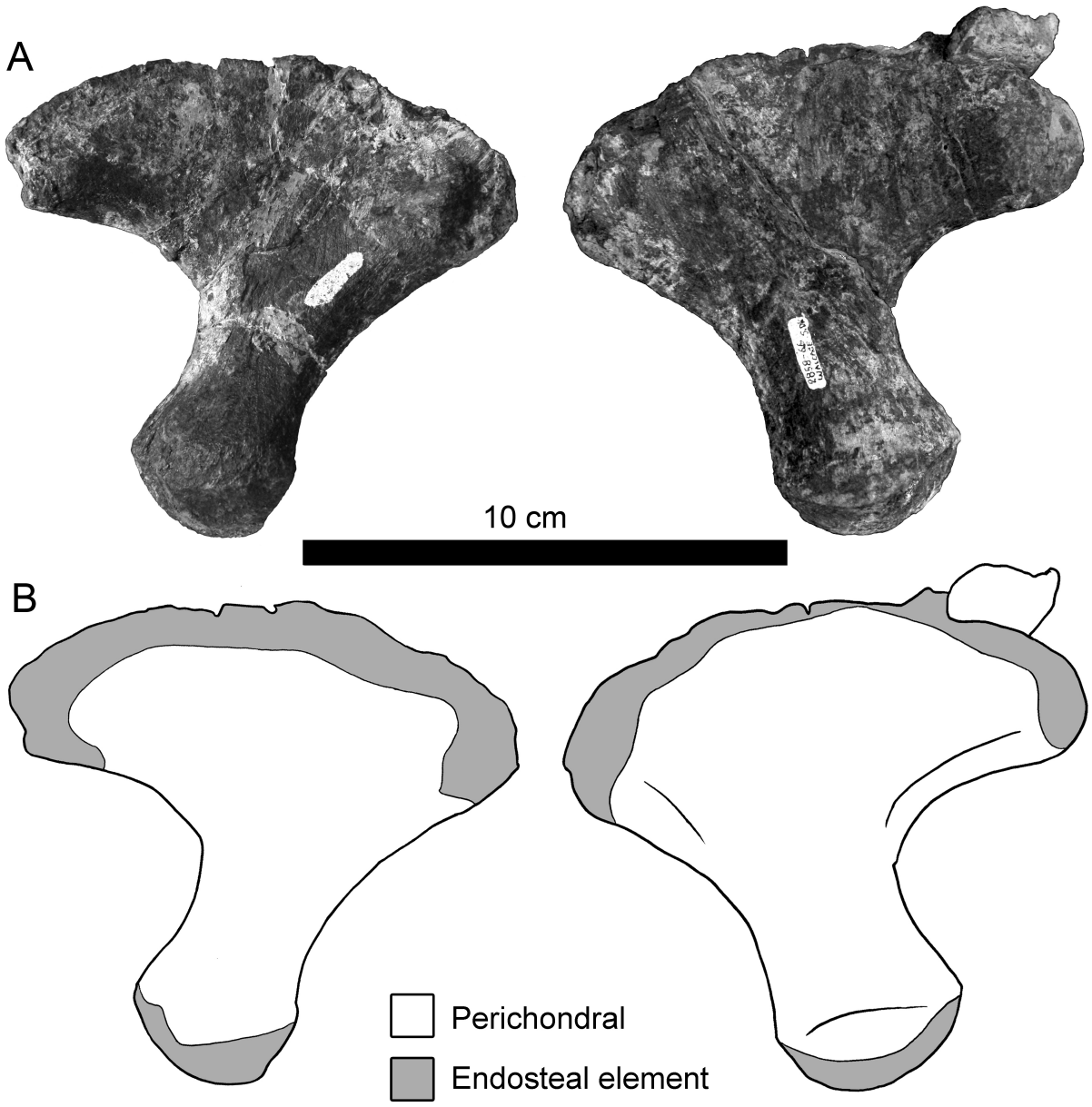

Figure 2.4. Scapulae osteological features-visceral. A) Visceral view of the left and right scapulae, respectively, of UNSM 55810. B) Schematic of the scapulae highlighting the endosteal element (gray) from the periosteal bone (white). The transition from endosteal to periosteal bone is noted by a distinct thickening of the bone along the anterior edge of the bone. There is also a roughened area of bone at the posterior end of the glenoid process, which may represent endosteal material that has not yet been covered with periosteal bone. The element along the anterior edge of the dorsal process is a phalanx that was not removed during preparation.

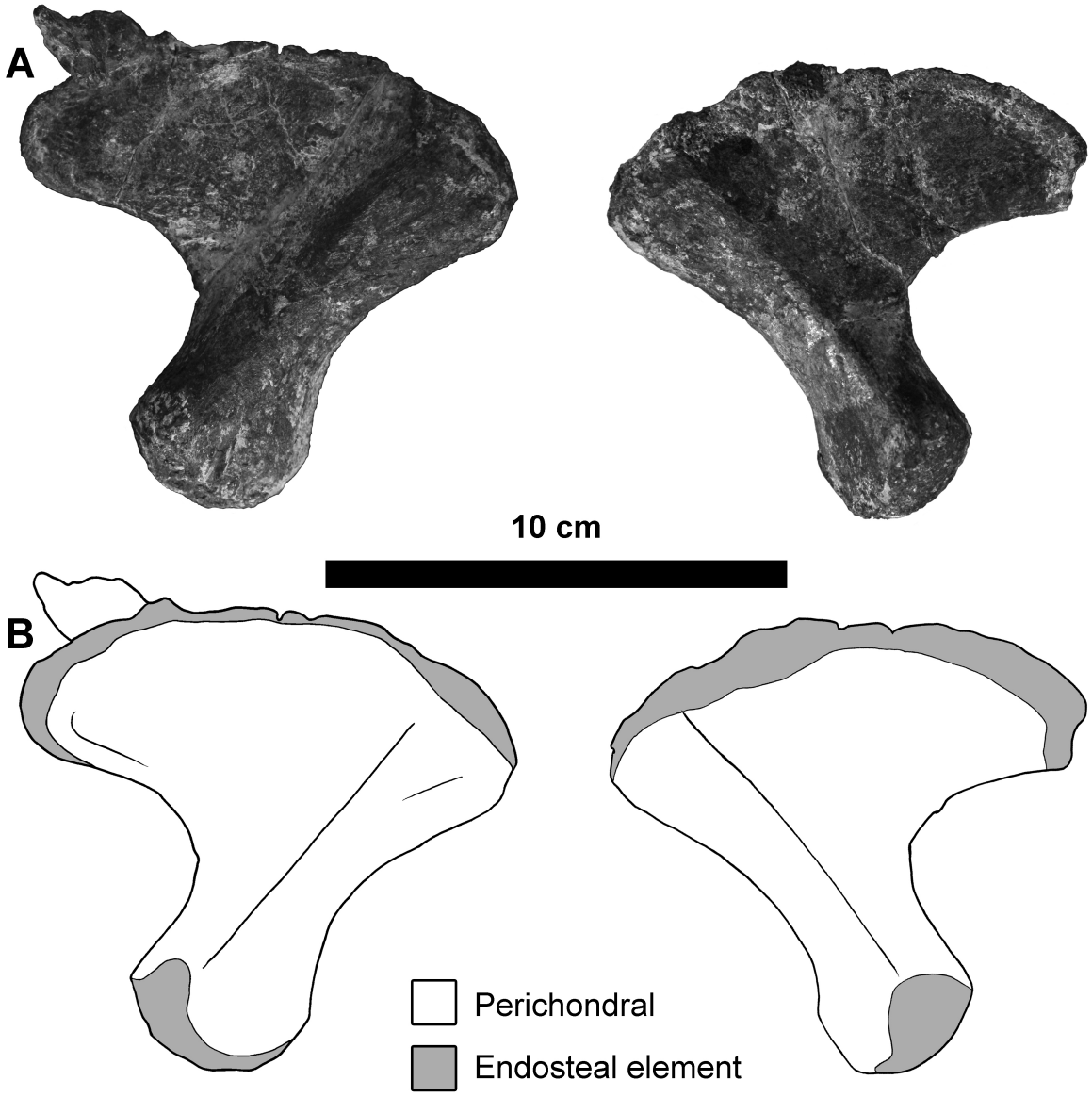

Figure 2.5. Scapulae osteological features-ventral. A) Ventral view of the right and left scapulae (respectively) of UNSM 55810. B) Schematic of the scapulae in ventral view highlighting the endosteal element (gray) as it differs from the periosteal bone (white). Note how a similar crest and thickening is present on the ventral side to that present on the visceral side of the scapulae. The endosteal element at the posterior end of the glenoid process continues around to the ventral side and follows up along the scapular ridge.

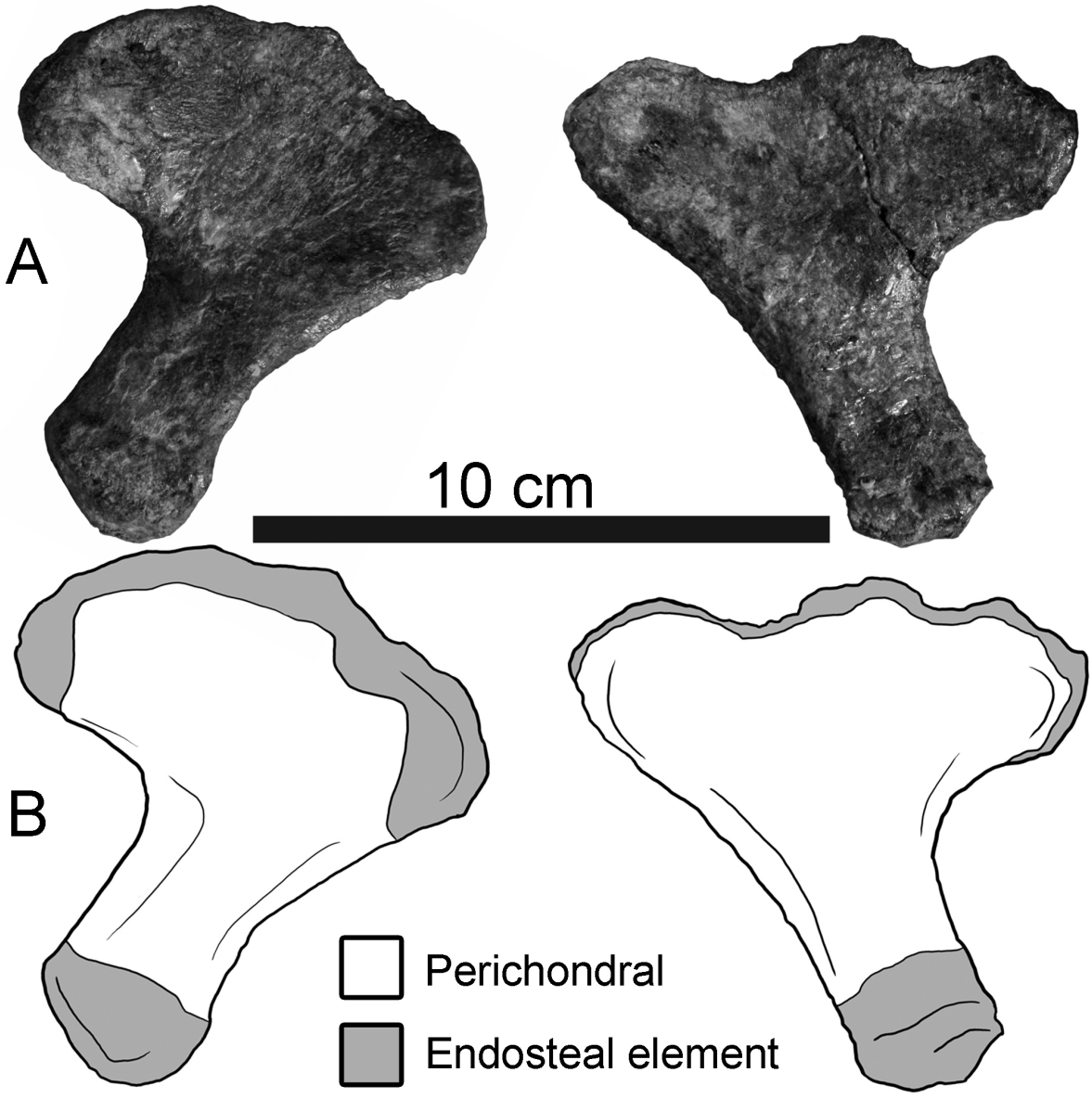

Figure 2.6. Fetal scapulae osteological features-visceral. A) Viseral view of the left and right scapulae, respectively, of LACM 129639b. B) Schematic of the scapulae illustrating the distinction between the endosteal element (gray) and the perichondral bone (white).

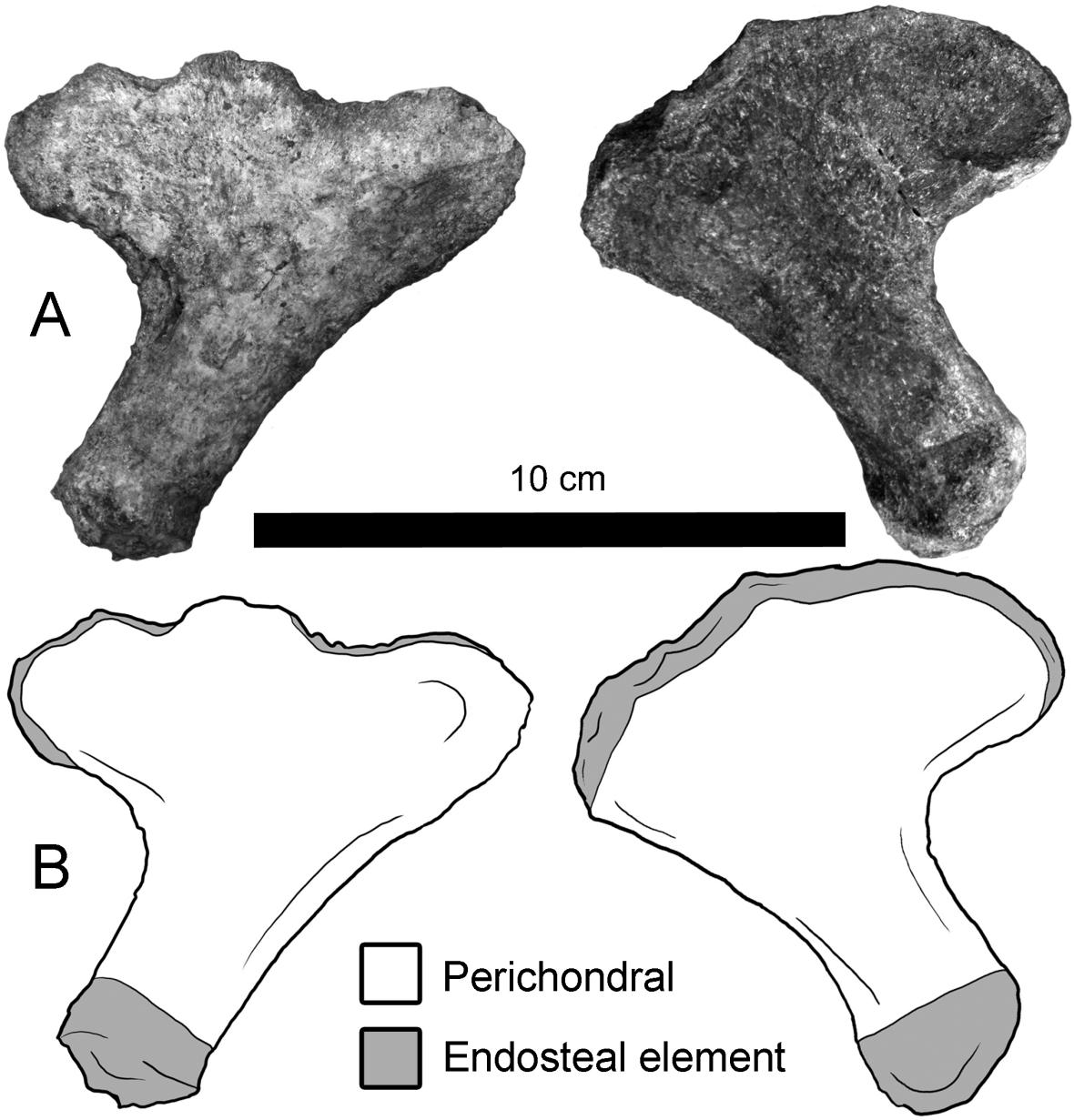

Figure 2.7. Fetal scapulae osteological features-ventral. A) Ventral view of the left and right scapulae, respectively of LACM 129639b. B) Schematic of the scapulae illustrating the distinction between the endosteal element (gray) and the perichondral bone (white).

Coracoids

The coracoids of the juvenile are primarily oval in shape with a prominent articulation area for the glenoid (Fig. 2.8B). Therefore, these bones lack anterior processes, the midline symphysis, and posterior extension and lateral elaboration. The irregular edge of the coracoids is continuous from the most anterior portion of the glenoid process around to the posterolateral edge. In addition, the irregular edge appears less well ossified than the interior of the bone, much like the anterior edge and transition from endosteal element to perichondral bone of the scapulae (Fig 2.9 and 2.10). Along the anterior portion, the bone is thickened extending from the glenoid prominence towards the midline. In addition, there is a concavity present on the lateral margins of the coracoids posterior to the glenoid prominence. The lengths are 136.5 mm for both the right and left coracoids of the juvenile. The width of the right coracoid is 121.5 mm and the left is 115mm.The morphology of the coracoids in UNSM 55810 is similar to that of the fetus but dramatically different from the adult polycotylid (Fig. 2.8).

The right coracoid of LACM 129639b, originally identified as the ischium by O'Keefe and Chiappe (2011), lacks the strongly waisted acetabular process that is present in the ischium of UNSM 55810 and other adult polycotylids and plesiosaurs (Fig. 2.8B). The coracoid of the fetus shares several characteristics with the juvenile, including an overall oval shape, weakly developed glenoid prominence, and poorly developed medial to posterior edge (Fig. 2.8A). These commonalities support my identification of the element as a coracoid and not an ischium. The fetus has a glenoid prominence that is not as well developed as it is in the juvenile and the perichondral bone appears less well ossified (Fig. 2.8A). In addition, the fetus lacks the lateral concavity found below the glenoid area on the juvenile and the adult polycotylids. The fetal

coracoid also possesses a similar transitional lip to that found on the juvenile coracoid (Fig. 2.11). The length of the fetal coracoid is 117mm and the width is 91mm.

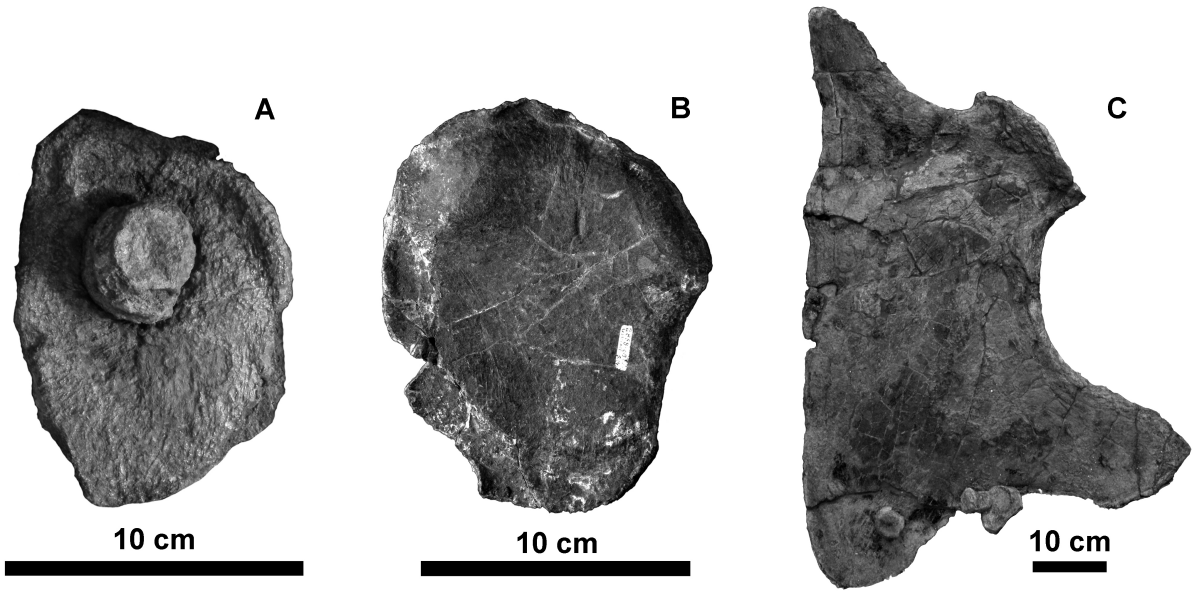

Figure 2.8. Polycotylid coracoid ontogeny. Visceral view of the right coracoid of the A) fetus (LACM 129639b), B) juvenile (UNSM 55810), and C) adult (LACM 129639a). The fetus and the juvenile have an overall oval shape, although the juvenile shows much more ossification, particularly along the anterolateral region, than the fetus does. Both bones lack many of the characteristics present in the adult condition, including the anterior, lateral, and posterior ventral processes. All bones are right coracoids shown in visceral view.

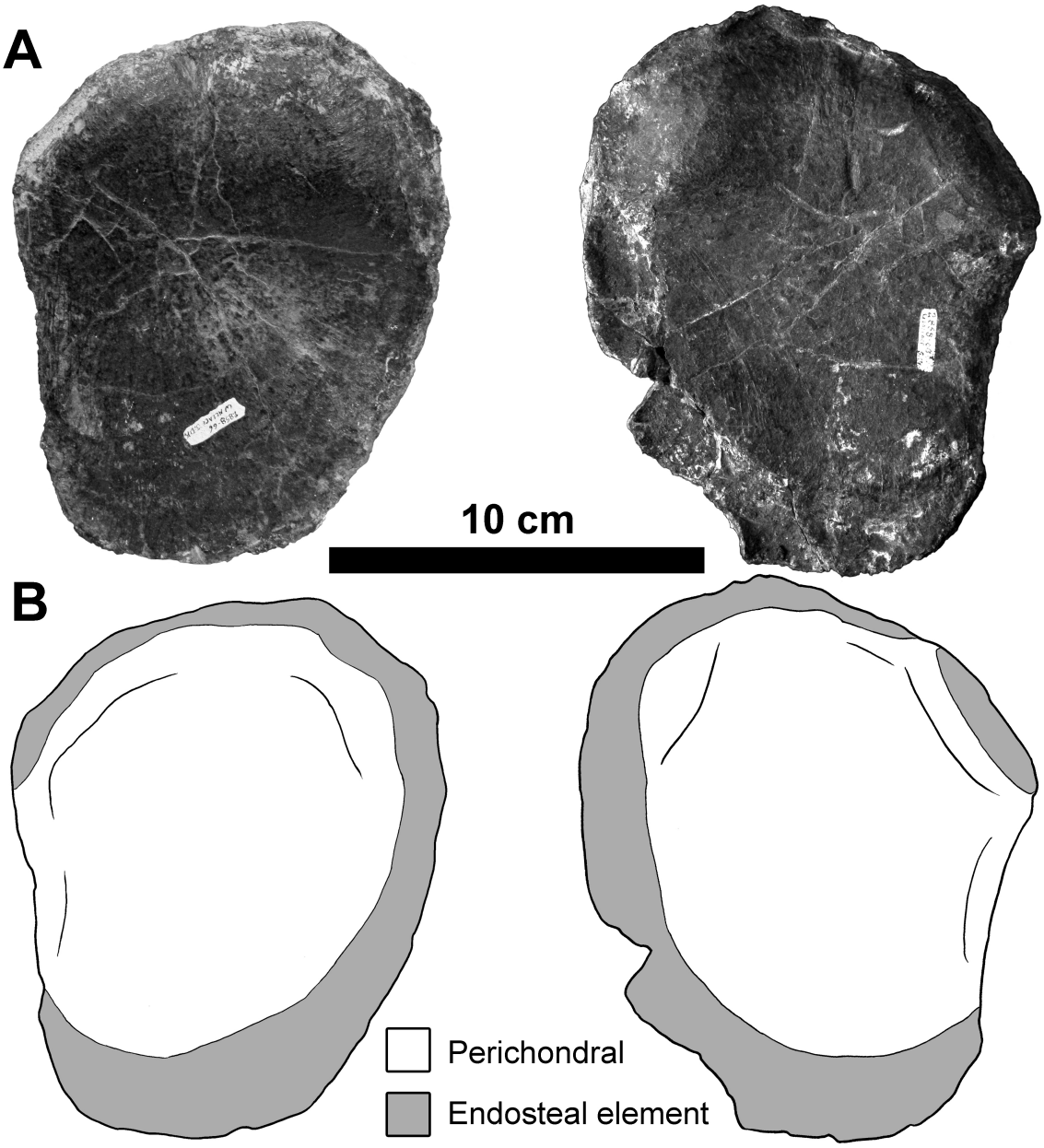

Figure 2.9. Coracoid osteological features-visceral. A) Visceral view of the left and right coracoids, respectively, of UNSM 55810. B) Schematic of the transition of endosteal element (gray) to perichondral bone (white) in visceral view. Note that the coracoids a similar roughness at the area for the glenoid fossa, much like the glenoid prominence of the scapulae. The lateral concavity has a pinched-off appearance much like the glenoid prominence but lacks the same lip and transition area as the rest of the bone.

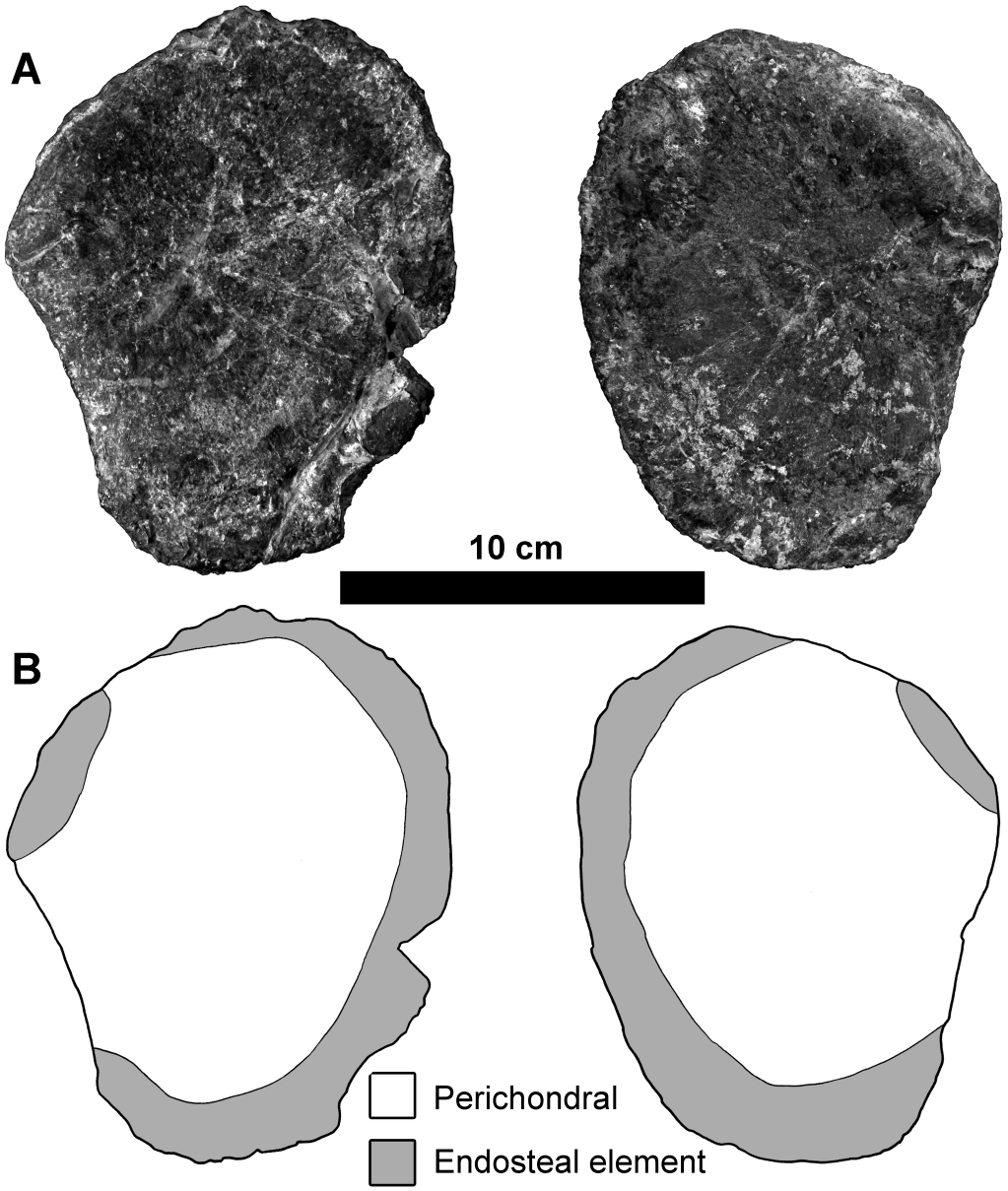

Figure 2.10. Coracoid osteological features-ventral. A) Ventral view of the right and left coracoids, respectively, of UNSM 55810. B) Schematic of the transition of endosteal element (gray) to perichondral bone (white) of the coracoids in ventral view.

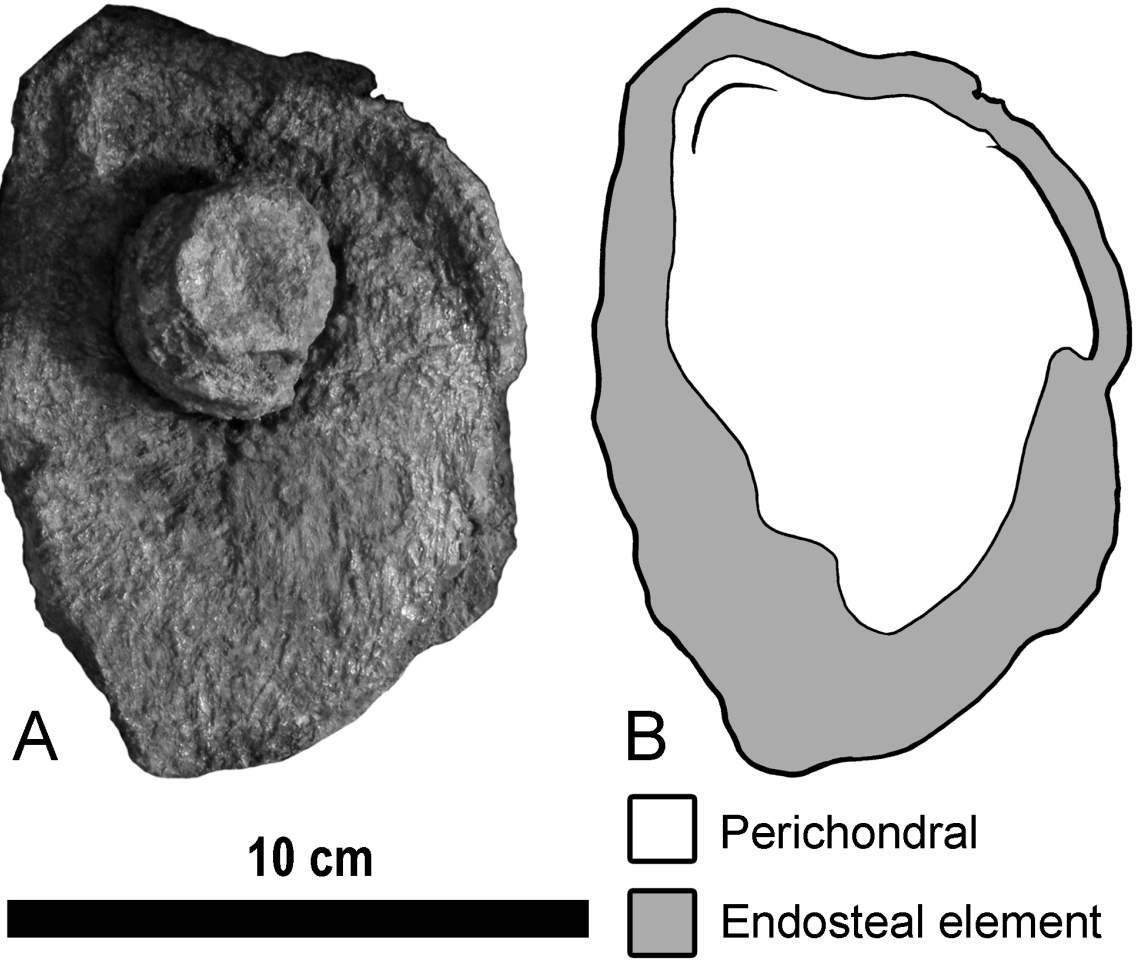

Figure 2.11. Fetal coracoid osteological features – visceral. Right visceral coracoid of LACM 129639b (A) and schematic of the endosteal element (gray) and the periosteal bone (white) (B). The coracoid of the fetus possesses a transitional lip similar to those found on the coracoids of UNSM 55810, indicating the transition from perichondral bone to the endosteal element. Therefore, endochondral ossification precedes perichondral ossification prior to birth.

Results: Pelvic Girdle

Pubes

The pubes are semi-circular, plate-like bones with a concavity along the posterior edge, forming the anterior edge of the puboischiadic fenestra (DallaVecchia, 2006). The anterior half of the bone is thin and gently rounded, while the posterior half is thickened at the area nearest the puboischiadic fenestra. Like the scapulae and coracoids, the pubes possess a variably widened lip of endosteal bone that precedes the perichondral bone visible on both the visceral and ventral sides (Fig. 2.12 and 2.13). The acetabular prominence extends posterolaterally and ends as a pinched-off mass. The right pubis of the juvenile has a length of 114 mm with a width of 123.5 mm. The left pubis has a length of 116.5 mm with a width of 114 mm.

The pubes of UNSM 55810 closely resemble the pubes of the fetus from LACM 129639b in regards to their semicircular shape and weakly developed anterior edge (Fig. 2.14A and B). In addition, the fetal pubes possess the transitional lip, much like the lip found in the juvenile pubes (Fig. 2.15). The lengths of the left and right pubes are 101.5 mm and 104 mm. The widths of the fetal pubes are 129mm and 120mm. When compared to the adult morphology of other polycotylids, the general plate-like form is conserved (Fig. 2.14C).

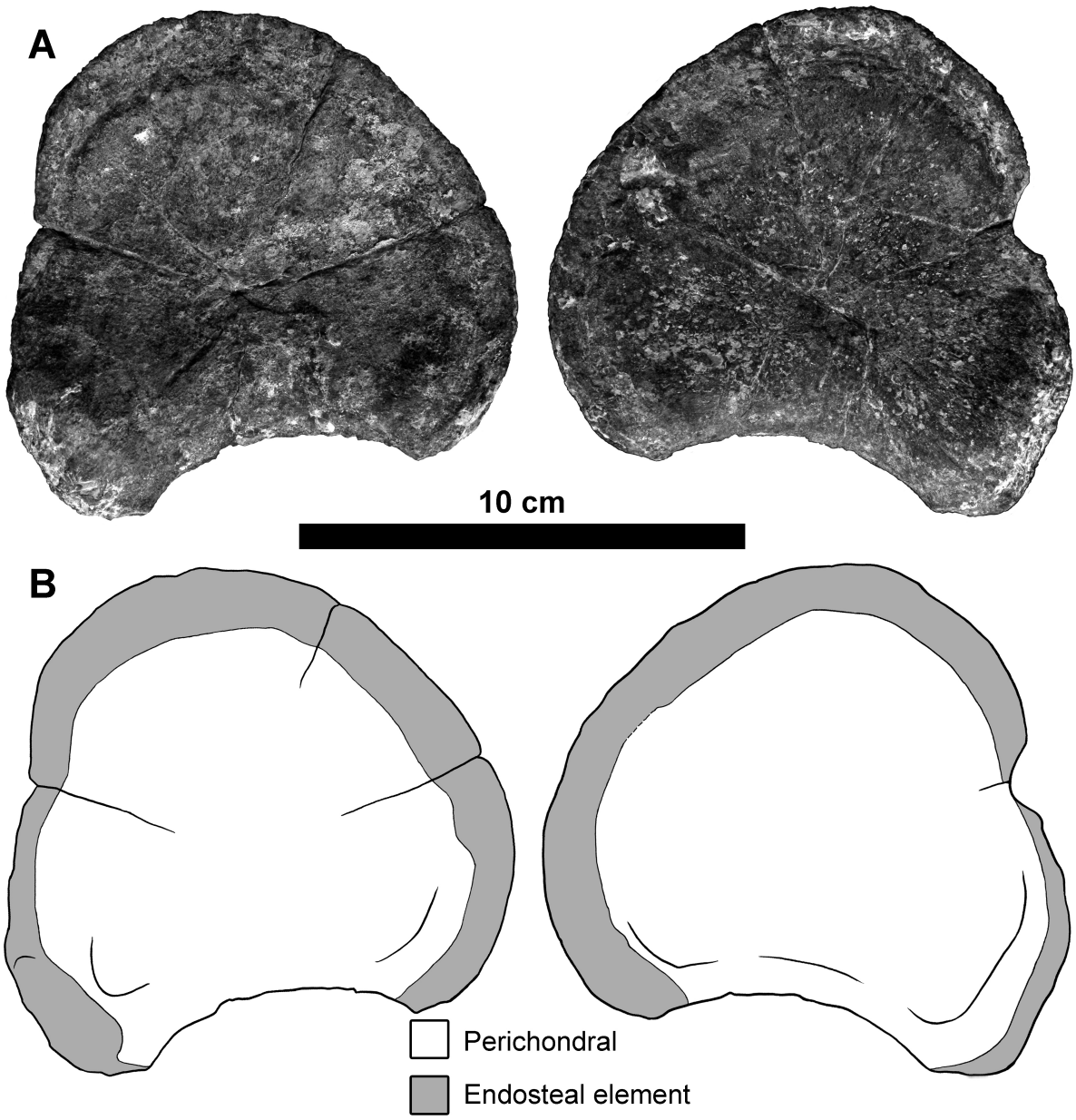

Figure 2.12. Pubes osteological features-visceral. A) Visceral view of the left and right pubes, respectively, of UNSM 55810. B) Schematic of the pubes demonstrating the extension of the endosteal element (gray) in relation to the perichondral bone (white). The endosteal element extends along the entire margin of the pubes with the exception of the margin for the posterior concavity. Much like the lateral edge of the coracoids of the juvenile, the pubes also have a pinched-off appearance and lack of the transitional lip.

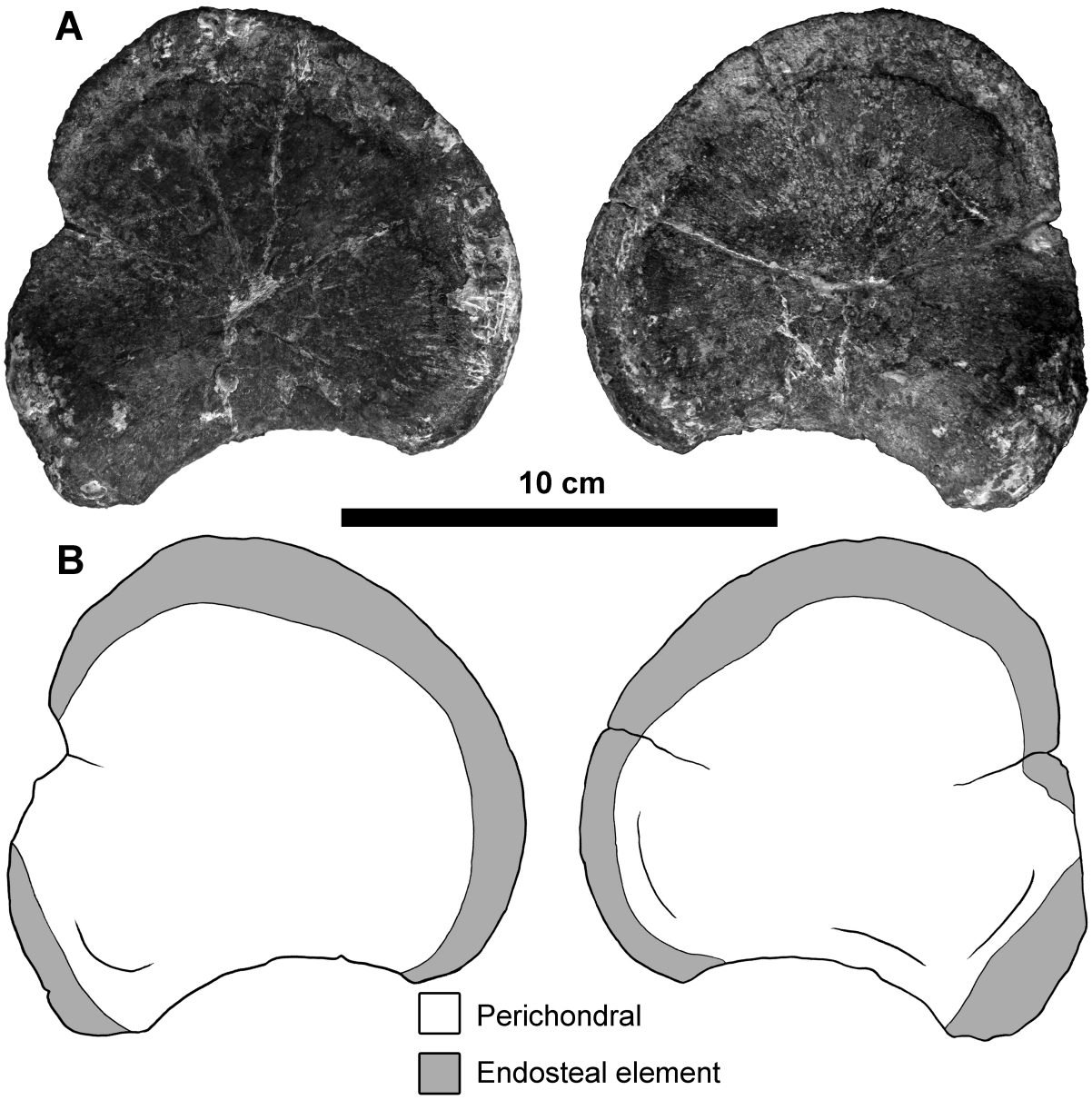

Figure 2.13. Pubes osteological features-ventral. A) Ventral view of the right and left pubes, respectively, of UNSM 55810. B) Schematic of the pubes outlining the extent of the endosteal element (gray) and the perichondral bone (white).

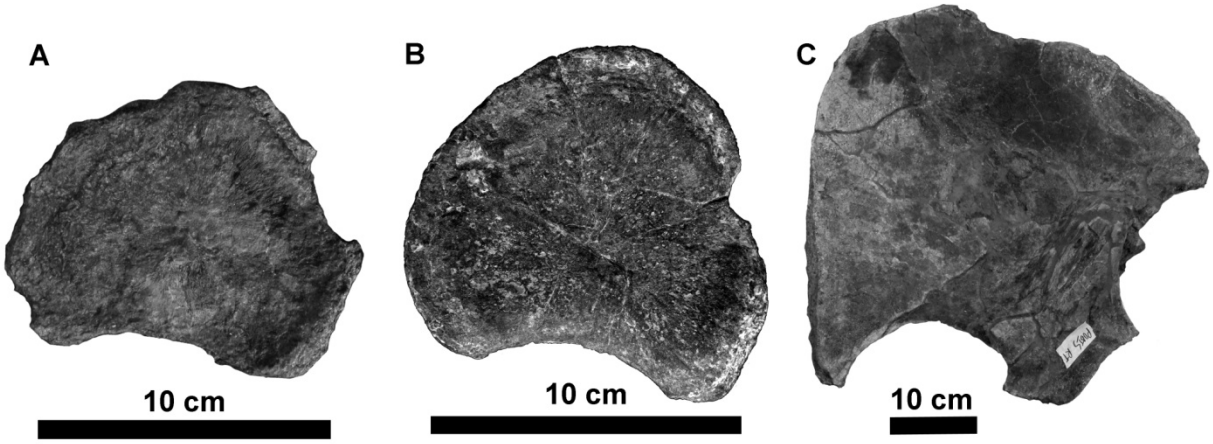

Figure 2.14. Polycotylid pubis ontogeny. Visceral view of the right pubes of the A) fetus (LACM 129639b), B) juvenile (UNSM 55810), and C) adult (LACM 129639a). Note relatively conserved plate-like shape throughout ontogeny. Into adulthood, there is elaboration on the lateral edge in the shape of a horn and a posterior process as the medial symphysis extends towards the ischia. All bones are right pubes shown in visceral view.

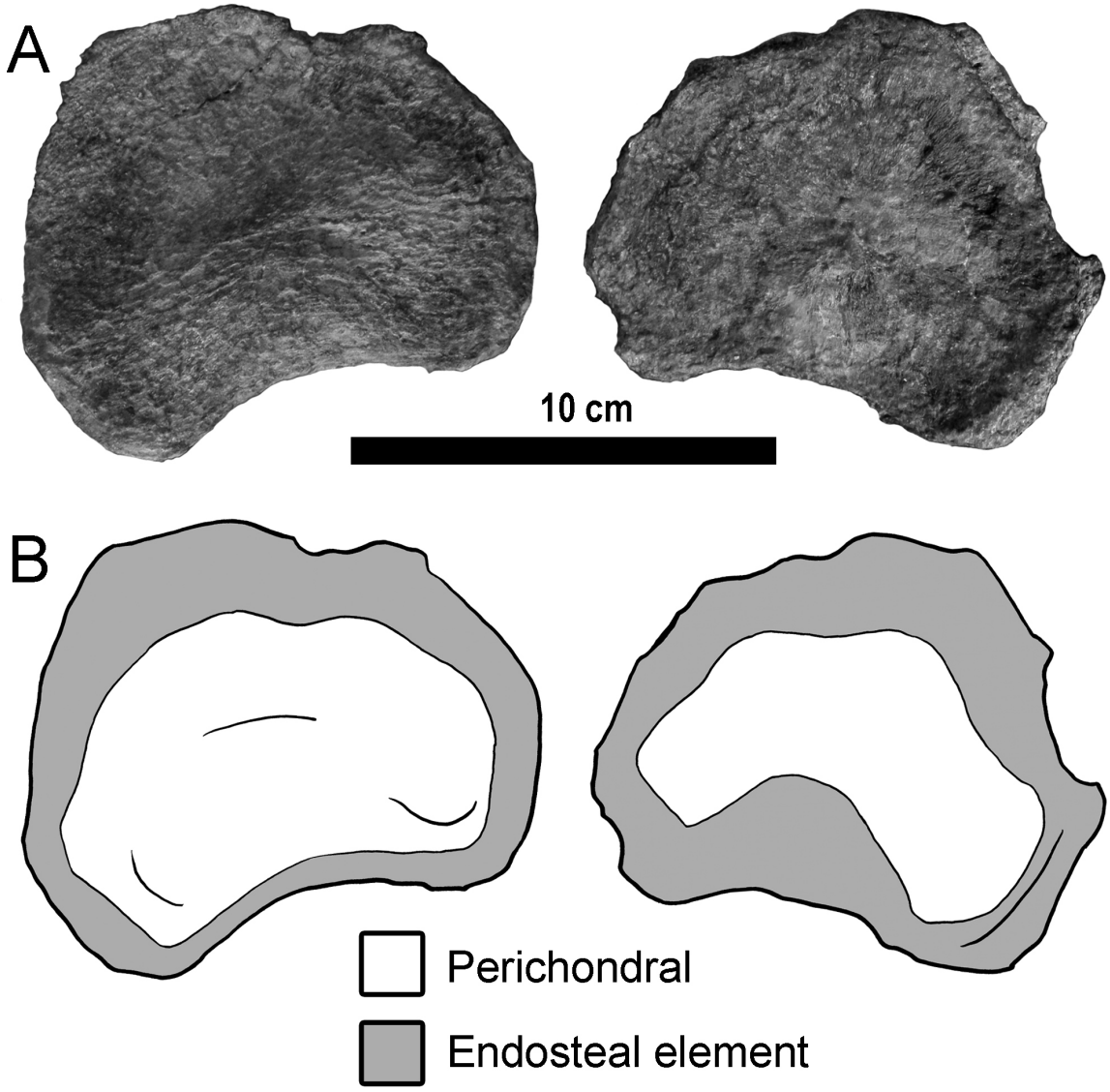

Figure 2.15. Fetal pubes osteological features – visceral. A) Pubes of the fetus (LACM 129639b) and B) a schematic of the endosteal element (gray) and the periosteal bone (white). The transitional lip is present around the perimeter of the pubes and supports that endochondral ossification preceded perichondral ossification *in utero* among polycotylids.

Ischia

The ischia are hatchet-shaped bones with waisting around the acetabular process, much like the adult condition in *Polycotylus* and several other plesiosaurs (Fig. 2.16). There is a

concavity along the anterior margin of the ischia that forms the other half of the puboischiadic fenestra. The acetabular process extends anterolaterally, ending as a pinched-off bulbous mass, similar to the glenoid process of the scapulae. In addition, the end of the acetabular process demonstrates differing thickness of bone along the process, wherein the bone on the ventral side is thicker than the visceral side. The only other bones of the juvenile that show this feature are the propodials. The ischia, too, have the transitional lip where the thin endosteal element precedes the perichondral bone, running from the most anteromedial area, along the medial edge to the posterior edge of the posterior ventral ramus on the visceral and ventral sides of the bones (Fig. 2.17 and 2.18). The ischia of the juvenile also have thickened anterior and posterior edges with bony prominences along the medial margin within the perichondral bone, while the medial edge remains thin. The right ischium has a length of 111 mm and the left is 110.5 mm. The widths of the ischia measure 105 mm for the right and 106.5 mm for the left.

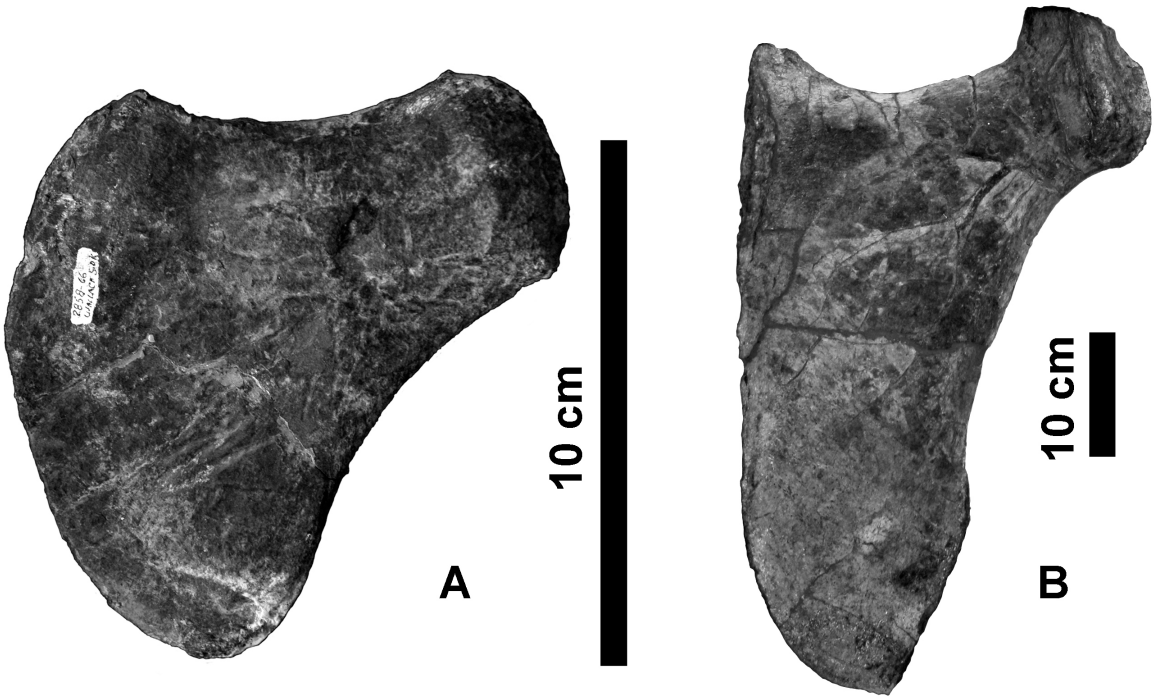

Figure 2.16. Polycotylid ischium ontogeny. Viscercal view of the right ischium of the A) juvenile (UNSM 55810) and B) adult (LACM 129639a). Note drastic elongation of the posterior ventral ramus. The ischia of the juvenile have waisting around the acetabular process, similar to that found in the adult specimen. The main differences between are the acetabular process ends as a rugose, pinched-off mass, there is not a median symphysis, and the posterior ventral ramus to proportionally short.

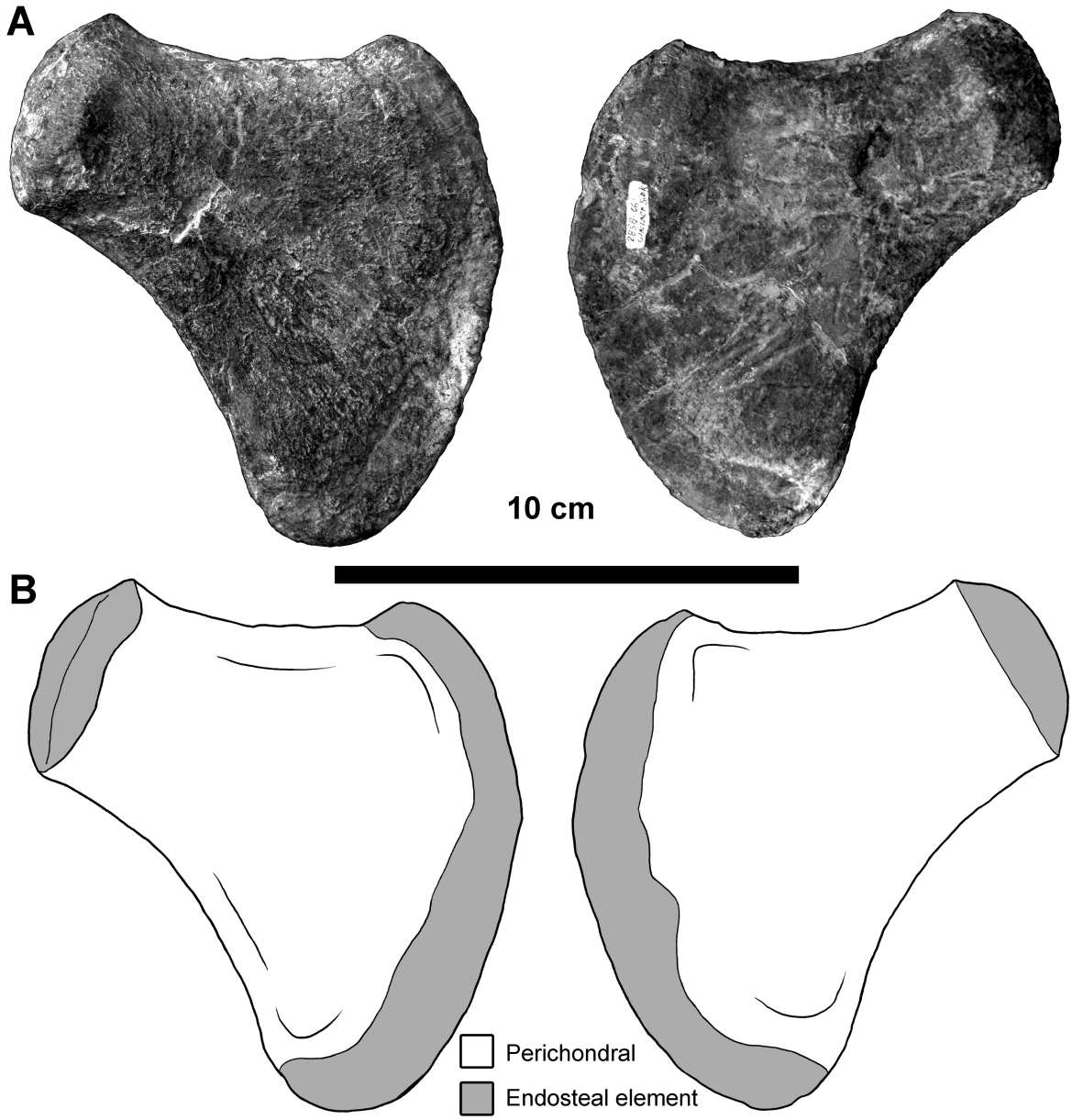

Figure 2.17. Ischia osteological features-visceral. A) Viseral view of the left and right ischia, respectively, of UNSM 55810. B) Schematic of the ischia illustrating the distinction between the endosteal element (gray) and the perichondral bone (white). Like the scapulae, the ischia lack the transitional lip along the two sides of the bone. In this case, the anterior and posterior edges appear better ossified and have a pinched edge.

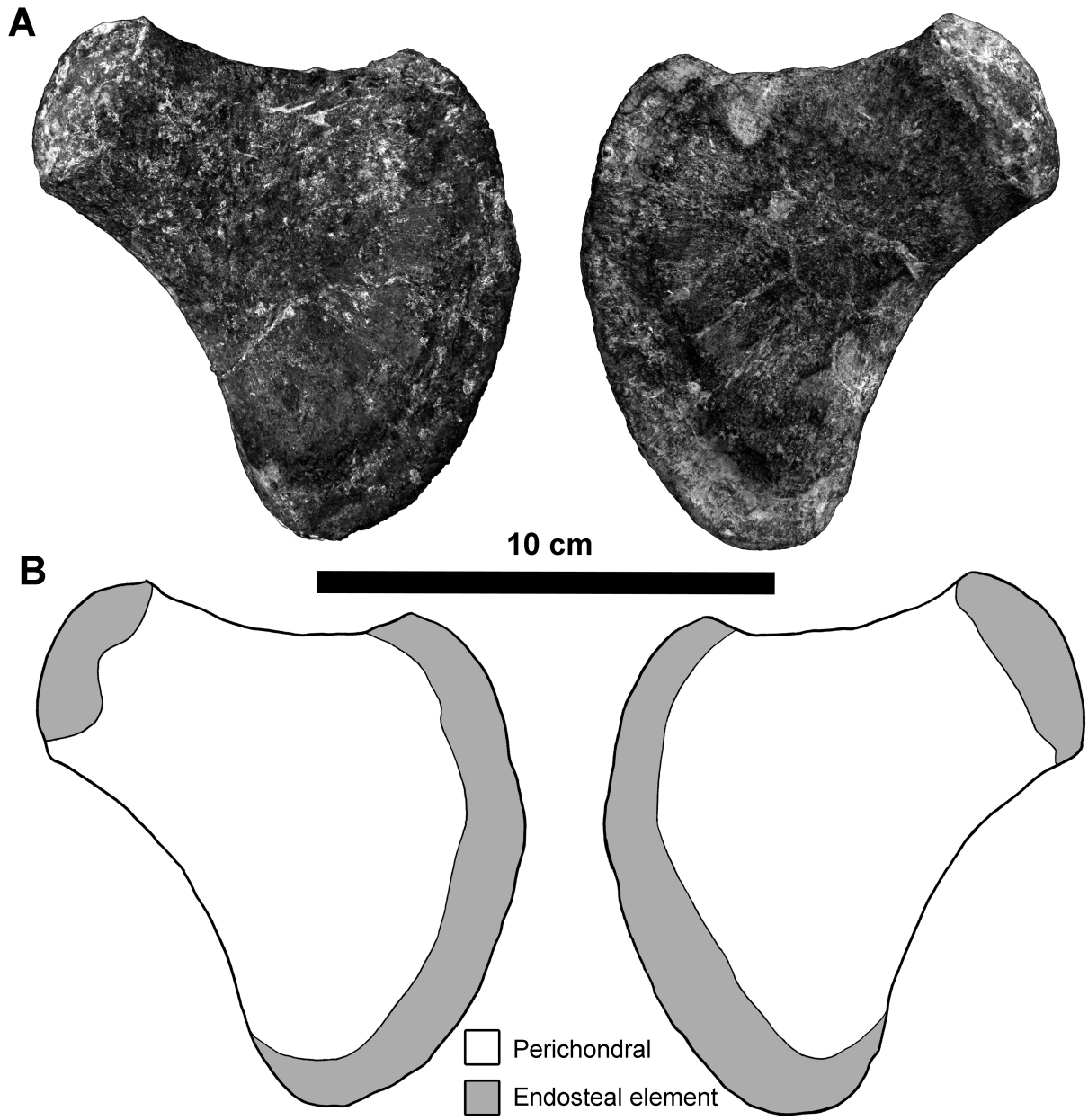

Figure 2.18. Ischia osteological features-ventral. A) Ventral view of the right and left ischia, respectively, of UNSM 55810. B) Schematic of the ischia illustrating a similar pattern of endosteal (gray) to perichondral (white) bone as that of the visceral side.

Ilium

The juvenile possessed one of its two ilia, which has a broad articulation area at the inferior end and tapers toward the superior end of the ilium. The ilium is relatively flat along

one side of the bone, while the other side has a curvature that accommodates the tapering of the bone. The ilium has a total length of 89.2 mm.

The ilia of the fetus, juvenile and adult polycotylids share a similar tapering superiorly, however, the fetus and adult do not appear to taper to the same degree as the juvenile (Fig. 2.19). The primary different between the juvenile and the fetus and adult ilia is the lack of a bend in the shaft. The bend in the shaft of the ilium is diagnostic to *Polycotylus* and helps to support the hypothesis that UNSM 55810 is of the genus *Dolichorhynchops* (O'Keefe and Byrd, 2012).

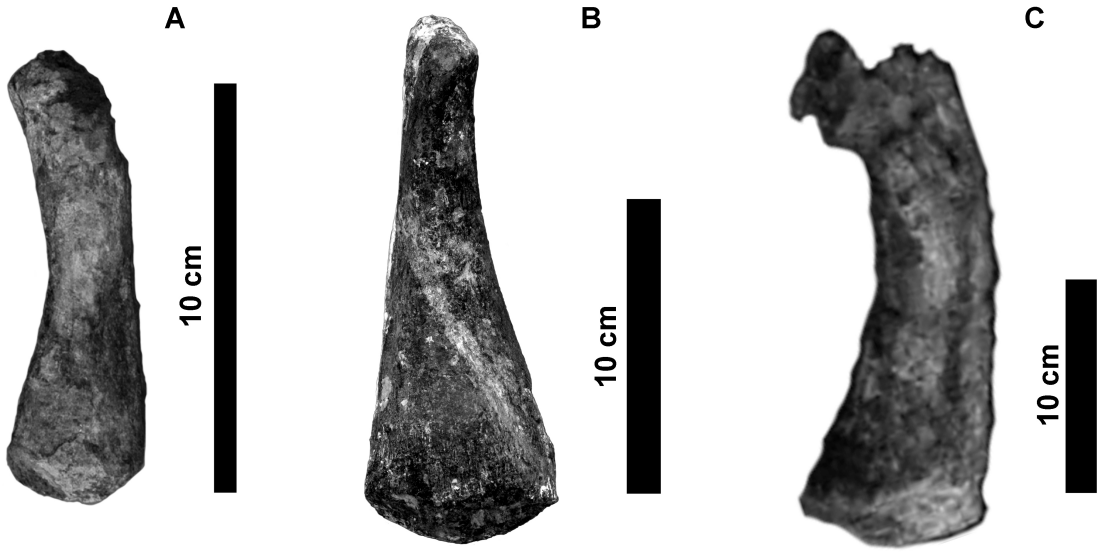

Figure 2.19. Polycotylid ilium ontogeny. A) fetus (LACM 129639b), B) juvenile (UNSM 55810), C) adult (LACM 129639a). Note that all the ilia have variable amounts of tapering and can vary taxonomically in regard to having a straight or bent shaft.

Allometric Growth of Polycotylid Plesiosaurs

Clavicles

Due to several of the clavicles missing one or more complete measurements, I was not able to execute a size/shape analysis. For now, the clavicles remain useful for qualitative comparison.

Scapulae

When the scapulae of the embryo and juvenile are compared to those of the adult and five other polycotylids from the genera *Dolichorhynchops*, *Polycotylus*, and *Trinacromerum*, we see a large amount of allometric growth occurring along the ventral ramus and dorsal process. I used a bivariate analysis to compare the logged widths and lengths of eight polycotylid plesiosaurs in order to determine significant amounts of allometric growth. When the scapular length (anterior to posterior) and width were analyzed, there was a significant amount of negative allometric growth (Fig. 2.20A). This suggests that throughout ontogeny, the scapulae become wider. However, the orientation of the scapula is anteromedial; therefore, the increasing width of the scapula is accounted for by the anteromedial growth of the ventral ramus and the lengthening of the dorsal process. I compared the anteromedial angle length against the width and found that there was not significant allometric growth (Fig. 2.20B). This suggests that the perceived allometric growth of the scapulae is actually a product of the anteromedial and posterolateral growth of the anterior ramus and dorsal process elongating to influence the measured width of the bone.

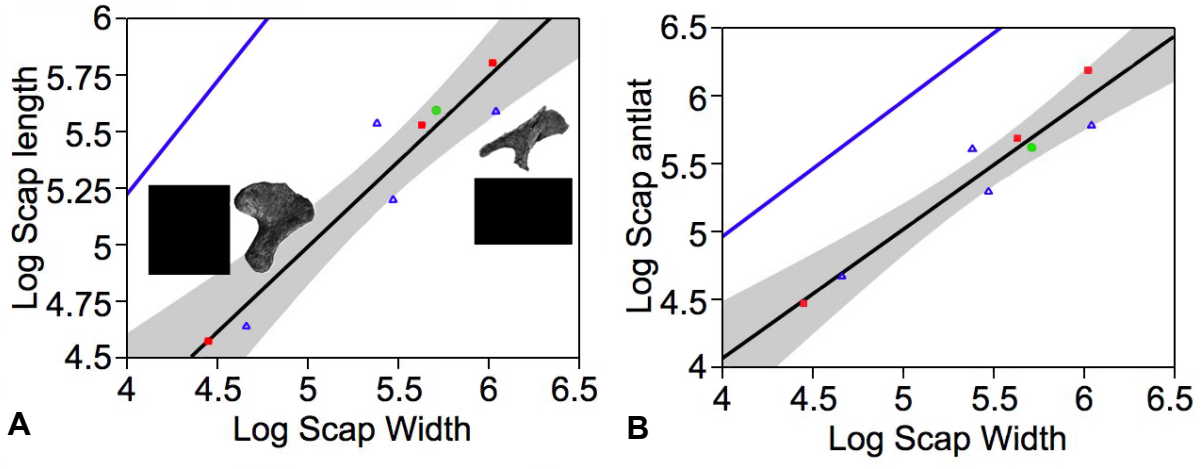

Figure. 2.20. Bivariate analysis of polycotylid scapulae. n=8 A) When comparing the length and widths of the scapulae, there was a statistically significant difference suggesting that there is negative allometric growth. Of the specimens included in this analysis, the fetus was the smallest and the adult was the largest. Slope = 0.7539±0.0997. B) When comparing the length from the most anteromedial point to the end of the dorsal process to the width of the scapulae, the results suggest that there is no significant allometric growth. Slope = 0.9499±0.1129. The black rectangles represent the scaled shape change based on length and width. Blue triangle = *Dolichorhynchops*, Green circle = *Trinacromerum*, Red square = *Polycotylus*. Grey, fitted shading represents the 95% confidence interval of the slope of the line. Blue line represents the line of isometry (slope=1, y-intercept same as regression line).

Coracoids

When the length and widths of the coracoids were compared among the eight specimens, the analysis suggests that there is a slightly positive allometry but the results were not statistically significant (Fig. 2.21). Although this analysis did not demonstrate significance when comparing length and width of these plesiosaurs, it is important to note that two factors were not included in the calculation of these measurements: length of the anterior process and length of the lateral process as it extends beyond the posterior point of the glenoid process. Because these features are lacking in the fetus and juvenile, they were not included in the analysis. However, these features do allude to a possible functional need for such elaborations on the bone.

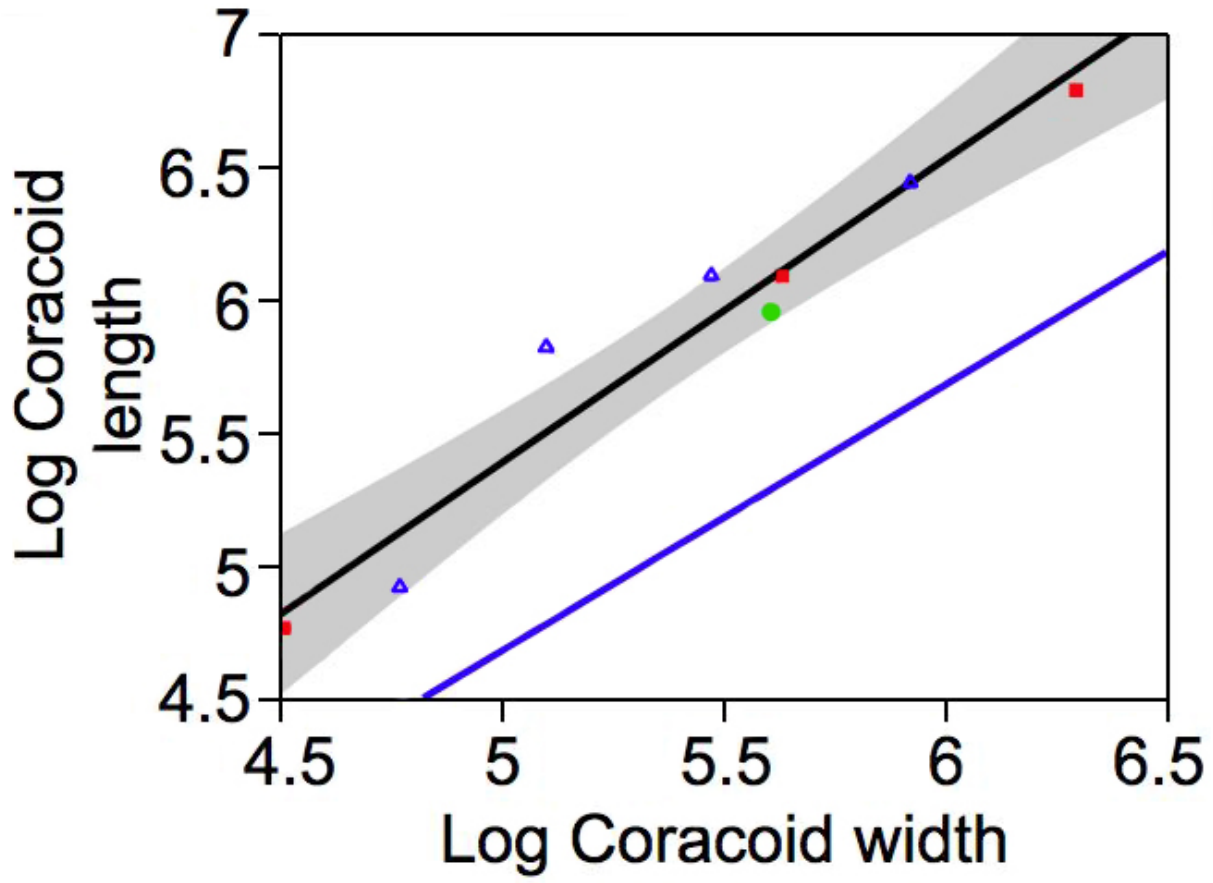

Figure 2.21. Bivariate analysis of polycotylid coracoids. n=8 The slope of the regression line suggests that there is positive allometric growth but it was not statistically significant. Slope = 1.1413±0.1159. Blue triangle = *Dolichorhynchops*, Green circle = *Trinacromerum*, Red square = *Polycotylus*. Grey, fitted shading represents the 95% confidence interval of the slope of the line. Blue line represents the line of isometry (slope=1, y-intercept same as regression line).

Pubes

The pubes also demonstrate a slightly positive allometry, but as with the coracoids, the results were not significant (Fig. 2.22). This lack of allometry reflects the conserved nature of the pubes. The main variation that occurs in the pubes is the location and amount of ornamentation (formation of various processes and prominences), just as in the coracoid.

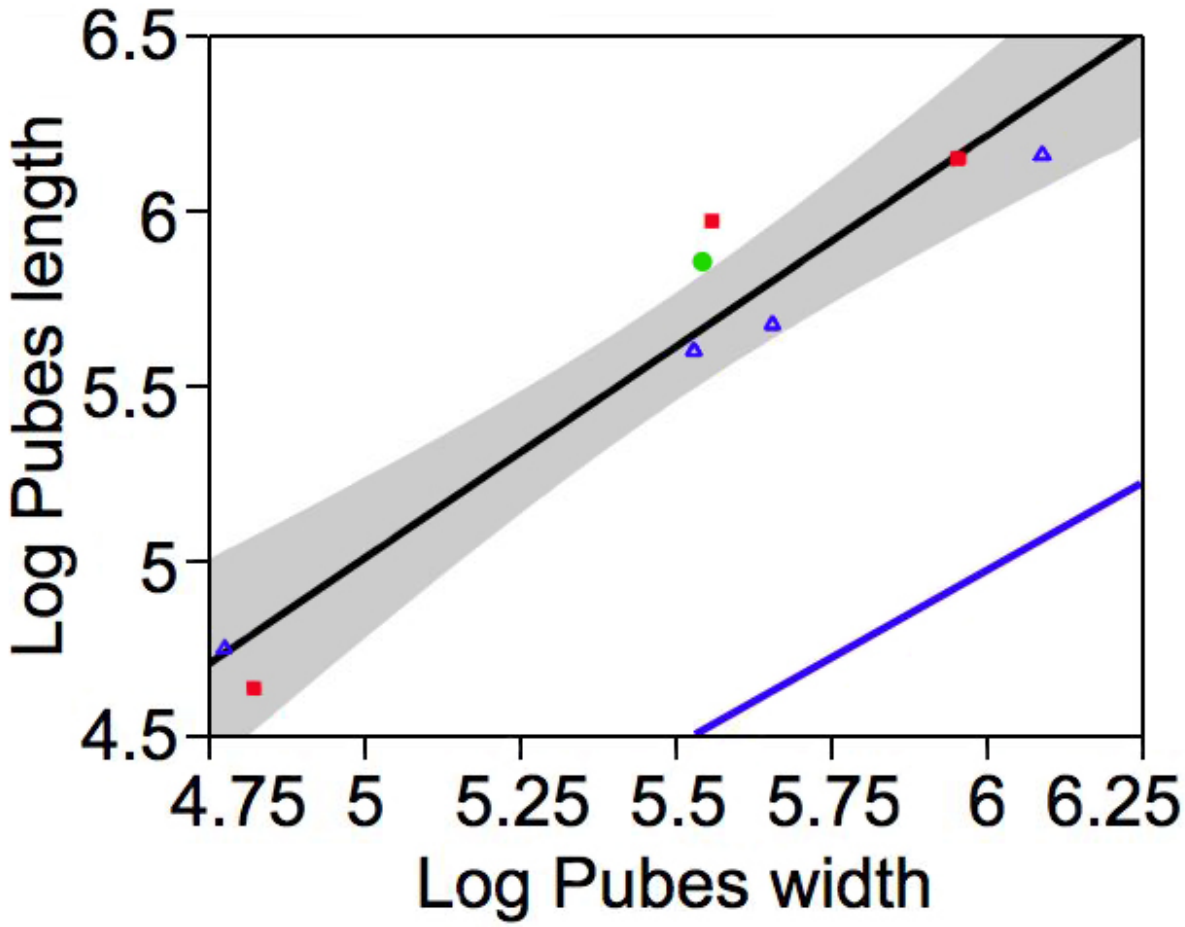

Figure 2.22. Bivariate analysis of polycotylid pubes. n=8 The slope of the regression line suggests that there is positive allometric growth, but it was not statistically significant. Slope = 1.2068±0.1419. Blue triangle = *Dolichorhynchops*, Green circle = *Trinacromerum*, Red square = *Polycotylus*. Grey, fitted shading represents the 95% confidence interval of the slope of the line. Blue line represents the line of isometry (slope=1, y-intercept same as regression line).

Ischia

For the ischia, seven specimens were compared due to the fetus (LACM 129639b) lacking either ischia. The results suggest a strong, statistically significant, positive allometric growth throughout ontogeny (Fig. 2.23). Elongation of the posterior ventral ramus was the dominant area of growth with some growth medially and laterally to contribute to increased width.

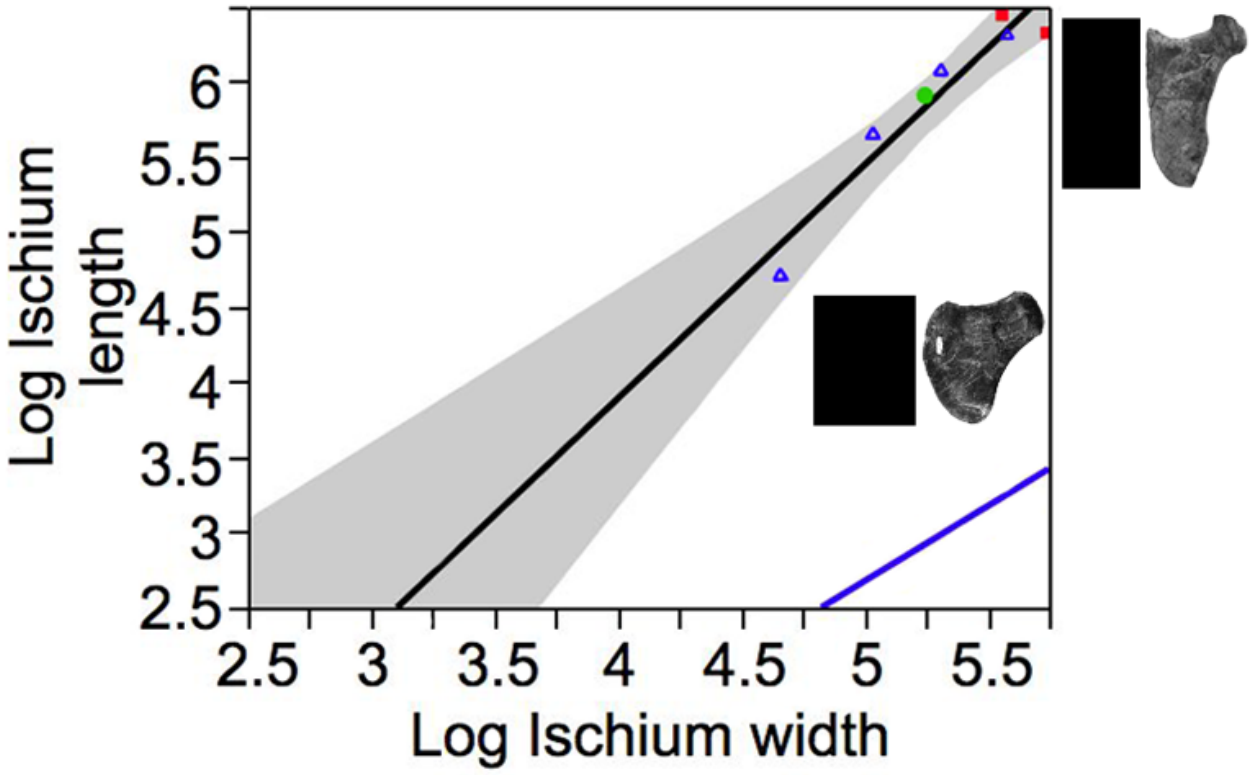

Figure 2.23. Bivariate analysis of polycotylid ischia. n=7 This analysis has one less specimen due to the fetus lacking either ischium. The results suggested that there was a statistically significant amount of positive allometric growth among the included polycotylids. From the seven specimens included in this analysis, the juvenile was the shortest and smallest, while the adult (LACM 129639a) was the largest and longest. Slope = 1.554±0.2109. The black rectangles represent the scaled shape change based on length and width. Blue triangle = *Dolichorhynchops*, Green circle = *Trinacromerum*, Red square = *Polycotylus*. Grey, fitted shading represents the 95% confidence interval of the slope of the line. Blue line represents the line of isometry (slope=1, y-intercept same as regression line).

Chapter 3

Throughout ontogeny, a plethora of variables influence the development of individuals and could contribute to the variation in morphology that I observed. For young plesiosaurs, their small size, the constraints of their environment, and the forces acting upon its body and bones, would influence the morphologies of the bones throughout ontogeny. Wolff's law suggests that bone shape is influenced by interactions with its mechanical environment (Pearson and Lieberman, 2004). This is accomplished via differences in mechanical loading as an individual grows, thereby increasing body mass (Pearson and Lieberman, 2004). In order for bones to compensate for increased body mass, they can respond in one or more ways: add bone mass, change the bone geometry to redistribute the stress that it must resist, and/or alter the microstructure of the bone (Pearson and Lieberman, 2004). This was a terrestrially based study but these same factors can also be applied to hydrodynamic forces in neutrally buoyant animals. I attempted to study the internal microstructure of the propodials of the juvenile. However, the bone was permineralized with metallics and other minerals that interfered with the microCT scan results. Therefore, of these three reactions, increasing bone mass and bone shape change are the primary factors that I will focus on in my discussion of polycotylid ontogeny. The focus of ossification of the bones is placed upon the areas of the body that are necessary for survival at birth (e.g. elements of the skull, vertebrae, and the areas closest to limb attachments for the girdle elements), while a leading edge of cartilage remains to be ossified later.

Conclusions and Discussion

The clavicles do not demonstrate morphological variation to the same degree as the other girdle elements. Instead, the morphology remains relatively conserved throughout the ontogeny

of polycotylids. Therefore, these bones tend to grow isometrically. This is beneficial because the triradiate shape is diagnostic to Polycotylidae, thereby supporting the identification of the juvenile to Polycotylidae.

Early in polycotylid ontogeny, the scapula appears to be more nothosaur-like than plesiosaur-like. The typical scapular condition of nothosaurs and pistosaurs consisted of a scapula possessing a broadened, well-developed glenoid ramus, a low, poorly developed dorsal process, and lacking a ventral ramus (Storrs, 1991; Sato et al., 2010), and is a condition mirrored in the early ontogenetic stages of polycotylids. As polycotylids continue to grow, the ventral ramus elongates and the morphology becomes more similar to that found in basal plesiosaurs such as *Plesiosaurus* and *Westphaliasaurus*. Therefore, the scapulae recapitulate sauropterygian phylogenetic history during ontogeny.

The greatest difference between the juvenile polycotylid scapulae and the scapulae of nothosaurs and pistosaurs is the anterior border of the ventral ramus. In the embryo and juvenile, the anterior edge of the ventral ramus is thin and irregular, whereas the basal sauropterygians have a thickened and smooth edge. The irregular edge suggests incomplete ossification of the scapulae and implies the presence of significant cartilage along the ventral ramus and anterior edge of the dorsal process for added support. Ossification of the scapulae is focused at the area of the glenoid ramus and its junction with the dorsal process. Therefore, at birth, the glenoid fossa is a functional joint that would enable the newborn to swim freely with the cartilage along the anterior edge and posterior end of the glenoid process, providing support for the anterior girdle until the ventral ramus and dorsal process are completely ossified (Fig. 3.1).

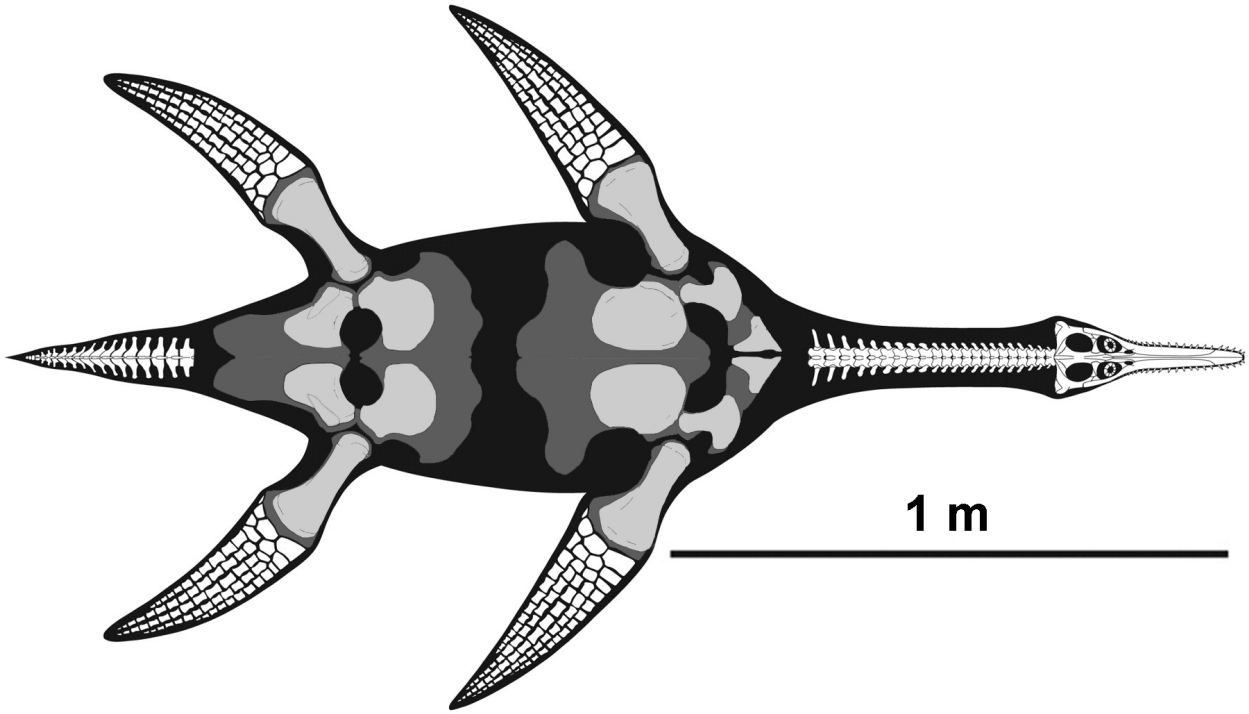

Figure 3.1. Schematic of possible extent of the cartilage in juvenile polycotylids. Light grey represents the morphology of early ontogenetic stage polycotylids, such as UNSM 55810 and LACM 129639b. The dark grey represents the adult morphology of polycotylids, such as that found in LACM 129639a. The dark grey indicates a possible extent of the cartilage that surrounded the girdle elements during development. However, the true extent of the cartilage is unknown and could span a variety of morphologies and extension throughout ontogeny. Note that the clavicle does not have cartilage due to its dermal origin.

The coracoids of UNSM 55810, most closely resemble those of *Placodus*, having a relatively reduced condition. However, UNSM 55810 does not possess a notch for an open coracoid foramen, as *Placodus* and *Keichousaurus* do (Rieppel, 1994). During ontogeny, the coracoids would grow together toward the middle, forming a symphysis, as well as hypertrophy anteriorly and posteriorly, resembling the condition found in *Westphaliasaurus*. In the near adult stage of development, the posterior growth elaborates to form the lateral horns common among the derived plesiosaurs such as *Cryptoclidus*, *Polycotylus*, and *Dolichorhynchops*. However, much like the scapula, the coracoid ossified nearest the glenoid. This is critical due to the need

for a functional glenoid fossa for swimming at birth. After birth, ossification and growth would occur along the cartilaginous lip and development of the various structures would occur (for possible cartilage extent, see Fig. 3.1). Cartilage would still be present at the glenoid process of the scapulae and glenoid protuberance of the coracoids in order to provide stabilization of the joint with the humerus and support muscle attachments.

Evidence of cartilage has been found not only in the juvenile (UNSM 55810), but also in the fetal specimen, LACM 129639b. The transitional lip is present, although not as strongly, around the perimeter of the scapulae, coracoids and pubes with varying widths. Presence of the lip in the fetus suggests that endochondral ossification precedes perichondral ossification *in utero* as well as in post-natal ontogenetic stages among polycotylids.

The overall morphology of the pubes of the juvenile closely resembles the juvenile condition in *Cryptoclidus oxoniensis* (Fig. 1.6) and the adult condition in *Westphaliasaurus* and *Microcleidus*. Among those taxa, the pubes have a semicircular, plate-like morphology and lack any elaboration along the anterolateral edge. As polycotylid ontogeny progresses, the pubis morphology starts to appear more cryptoclidid with the extension and development of the anterolateral edge, forming a lateral horn. Among polycotylid adults, the lateral horn is a common structure, as well as an anterior protuberance in *Polycotylus* (Fig. 2.18C). These bony elaborations do have the potential to be present in cartilaginous form as suggested in Fig. 3.1 or be absent and the cartilage remain a semi-circular shape following the shape of the ossified bone until late in ontogeny.

The hatchet-like shape of the ischia is reminiscent of the condition found in nothosaur-grade sauropterygians and basal plesiosaurs, such as *Nothosaurus* and *Cryptoclidus*. This shape along with the relatively short posterior ventral process is conserved throughout much of the

sauropterygian phylogeny until the evolution of polycotylids (Fig. 1.4). With polycotylids came the elongation of the ischia while the neck shortened. However, this is a common occurrence with pliosauromorph marine reptiles (Williston, 1903; O'Keefe, 2002; O'Keefe and Carrano, 2005). This reoccurrence of the short ischia in the fetus and juvenile helps to support the idea of polycotylid ontogeny recapitulating sauropterygian phylogeny. As with the other girdle elements, cartilage is present to an unknown extent. The extension of the cartilage could have maintained a morphology similar to the ancestral state, remaining relatively short and following the shape of the calcified cartilage and bone or been elongate along the posterior edge like the adult morphology (Fig. 3.1). Extension of the cartilage could not only provide support to the body and limb articulations, but also allow additional surface area for muscle attachments.

Form and Function

As the plesiosaur develops, the stresses on the bones change as body size and shape changes (Pearson and Lieberman, 2004). The stresses placed upon the bones would promote ossification of the cartilage, as it is needed to resist compression of the bone. As stress is applied via mechanical loading, it is distributed differently among the various bones of the body. Therefore, each bone would respond differently to a given stress, or not respond at all (Pearson and Lieberman, 2004). During ontogeny, if a stress is great enough to be detected by the skeletogenic cells (such as osteoblasts, osteoclasts, and chondrocytes), then these cells would begin to produce a collagen matrix, creating the framework for the basic histological form for the bone (Farnum, 2007). As this framework is laid down, the bone can add mass and maintain its original shape to resist the new stress, or the framework could develop a morphology that differs from the original form.

During polycotylid ontogeny, changing the shape of the bone appears to be the primary process that the skeletal elements utilize to resist mechanical loading. As described earlier, the polycotylid scapulae start as relatively short, hatchet like bones but during growth (as body mass increases), the bone changes shape, becoming more elongate anteromedially and posterolaterally (Fig. 3.1). Anteromedial elongation of the ventral ramus may be attributed to increased mechanical loading on the muscles that attach to the anterior portion of the bone. As body mass increases, more force is needed to propel the body forward through the water. Therefore, increased loading on the humerus will directly influence the associated muscles causing them to grow. With this muscle growth, pull of the muscle on the bone could cause enough stress to initiate bone growth and lead to a change in the shape of the bone in order to redistribute the stress from the added force (Pearson and Lieberman, 2004). Force along the subcoracoscapularis, which may be connected along the posterior edge of the scapula and anterior edge of the coracoid (Robinson, 1975), may aid in causing bone growth that draws the bone medially, broadening the ventral ramus and helping to widen the scapula as a whole. Force on and stress caused by the subscapularis (attaches along the medial area of the scapula) may influence the lengthening in the anteromedial direction of the scapula.

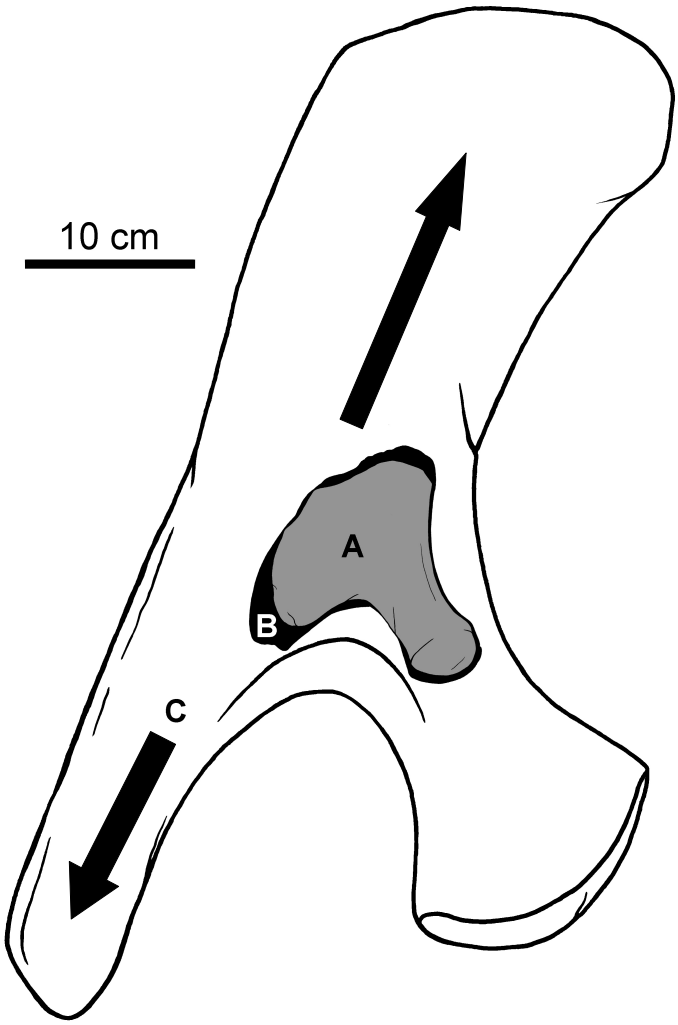

Fig. 3.2. Directions of allometric growth. The left scapula in visceral view of the A) fetus (LACM 129639b), B) juvenile (UNSM 55810), and C) adult (LACM 129639a; modified from O'Keefe and Byrd, 2012). The greatest amount of growth (represented by the black arrows) in the scapulae is occurring along the ventral ramus going anteromedially and the dorsal process, extending posterolaterally. Growth in these directions may be based on the muscles that attach along the ventral ramus.

The coracoids and pubes of polycotylids show similar trends of adding bone elaborations along specific edges. For the coracoids, lengthening and widening of the coracoid is likely occurring due to growth and use of the subcoracoideus, supracoracoideus, subcoracoscapularis, coracobrachialis, and pectoralis. The triceps may originate at the posterior edge of the glenoid region and the resultant force of the triceps on this joint may influence the robust nature of the

region. The pull on the pectoralis muscle potentially is the influence of the posteromedial horn of the coracoid and the formation of the midline symphysis. However, it is unclear to me what is influencing the posterolateral horns of the coracoid. Perhaps it is continued growth and extension of the subcoracoideus and/or coracobrachialis, but there may also be a muscle or ligament attached at the end. This second hypothesis could be ruled out due to a lack of a muscle scar or any kind of tuberosity on that area of the bone.

The ischia do illustrate an allometric growth and shape change. One of the muscles that may play a role in the extension posteriorly of the ischia is the ischiotrochantericus.

Pattern of Propodials

The propodials illustrate a dominance of the perichondral when compared to the pelvic elements. However, the propodials have different constraints on them than the girdle elements do. The girdle elements are growing within a body cavity and the main constraints are the extent to which the elements can grow until they hit one another and the extent anteriorly and posteriorly that muscle attachments influence the bone for growth. The propodials on the other hand are developing within a constrained cavity (the flipper). Muscle attachments are likely influential in the development of the propodials much like they are in the girdle elements, but the juvenile propodials demonstrate perichondral bone dominance around the long axis of the bones. Along the proximal and distal ends of the propodials, there is extension of the endosteal element (Fig. 3.2).

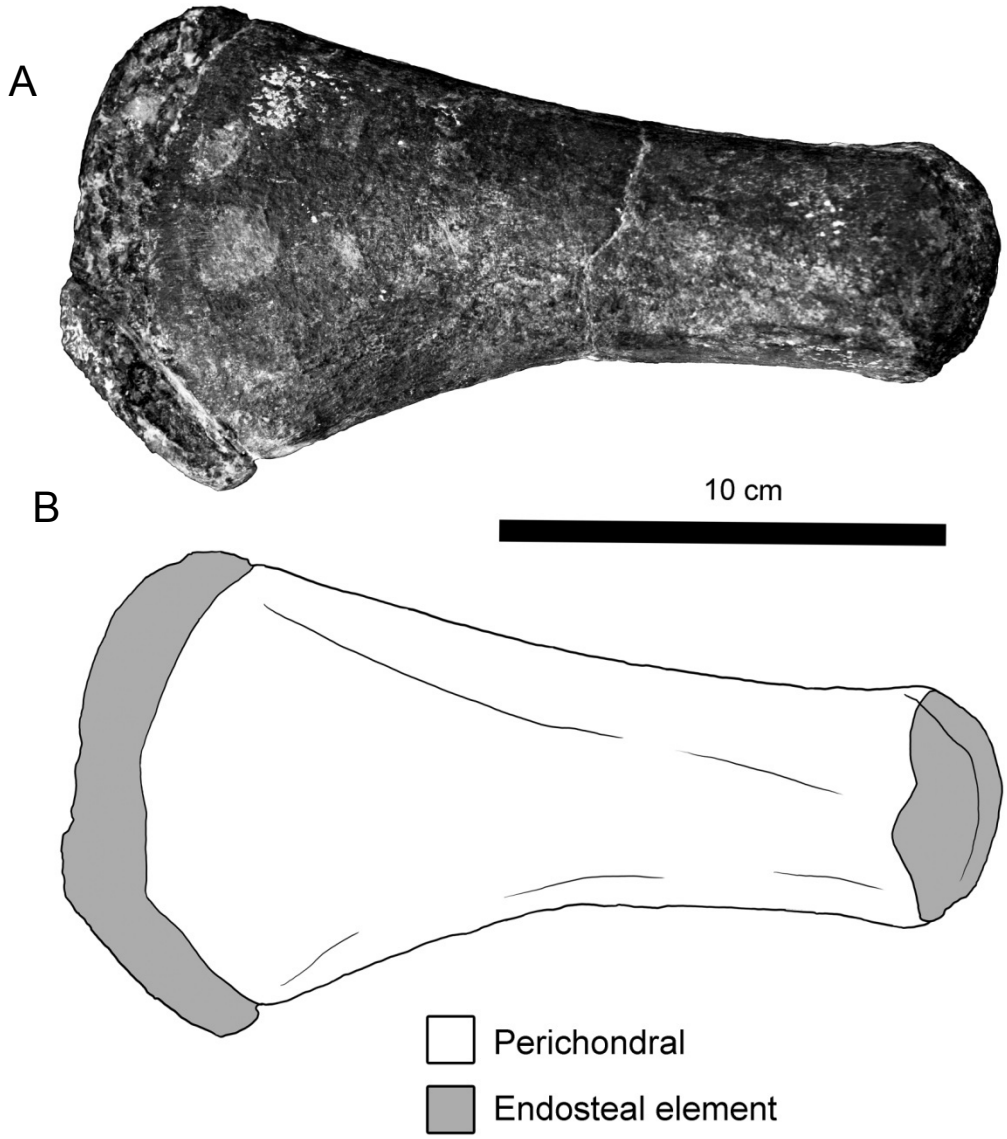

Figure 3.3. Propodial osteological features. A) Propodial of UNSM 55810. B) Schematic of the endosteal element (gray) and the periosteal bone (white) of the propodials. Note that there is a similar extension of endosteal element that precedes perichondral ossification.

By way of thorough inspection of the juvenile girdle elements and comparison with other polycotylid and sauropterygian specimens, I was able to note the primary differences in bone morphologies among polycotylids and how those morphologies related to ancestral sauropterygians. The changes that occurred throughout the ontogeny of polycotylids resembled

the pattern observed during the evolution of sauropterygians. The conservation of the ancestral form may be due to developmental canalization, wherein the evolutionary history of the animal is dictating the developmental form. However, the overall changes that occur are steeped in adaptation to a transition in environment. As basal sauropterygians moved from terrestrial and semi-aquatic locomotion to a fully aquatic lifestyle, certain changes occurred throughout the skeleton. Metric data allowed for quantification of these morphological changes.

Of the four girdle elements of primary interest (e.g. scapula, coracoid, pubis, and ischium), two illustrate allometric growth while the other two appear to grow isometrically. Understanding the metric differences of the bones is helpful, however, material that does not preserve easily should be considered as well. Cartilage was likely a major player during the development of polycotylid plesiosaurs and its presence is evident due to the transitional lip on the girdle elements of UNSM 55810 and LACM 129639b, suggesting a family level developmental feature.

Future work:

Additional work to be done on this specimen will include a detailed description of the cranial elements, the propodials, and other fragmented material that was preserved. Studying the cranial anatomy of the juvenile (UNSM 55810) will provide a rare look at polycotylid cranial ontogeny. Also, histological studies should be conducted on the girdle elements for better understanding of bone type and ossification patterns.

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Appendix A

Table 2.1. Specimen reference list. Measurements were made in millimeters (mm). Ant-Lat refers to the anterior to lateral measurement of the scapulae.

Specimen	Taxon	Scapula Left Length	Scapula Right Length	Scapula Average Length	Scapula Left Width	Scapula Right Width	Scapula Average Width	Scapula Left Ant-Lat	Scapula Right Ant-Lat	Scapula Average Ant-Lat	Coracoid Left Length
KUVP 1300	*Dolichorhynchops*	190	170	180	244	234	239	195	200	197.5	330
KUVP 40002	*Dolichorhynchops*	266		266	444	400	422	347	297	322	626
LACM 129639a	*Polycotylus*		330	330		413.8	413.8	483		483	
LACM 129639b	*Polycotylus*	98	95	96.5	88	84	86	83.5	90	86.8	
UNSM 55810	*Dolichorhynchops*	104.5	101.5	103	105.5	107	106.3	105.5	106.5	106	136.5
VP 12059	*Trinacromerum*	262	273	267.5	299	308	303.5	271	276	273.5	372
VP 404	*Dolichorhynchops*	264	241	252.5	205	232	218.5	276	265	270.5	439
YPM 1125	*Polycotylus*			250.7			280			293	

Specimen	Coracoid Right Length	Coracoid Average Length	Coracoid Left Width	Coracoid Right Width	Coracoid Average Width	Pubis Left Length	Pubis Right Length	Pubis Average Length	Pubis Left Width	Pubis Right Width	Pubis Average Width
KUVP 1300	343	336.5	155	174	164.5	273	265	269	253	252	252.5
KUVP 40002	622	624	375	372	373.5	468	474	471	447	437	442
LACM 129639a	883	883		543	543		467	467		385.7	385.7
LACM 129639b	117	117		91	91	101.5	104	102.8	129	120	124.5
UNSM 55810	136.5	136.5	115	121.5	118.3	116.5	114	115.3	114	123.5	118.8
VP 12059	396	384		273	273	347.5		347.5	256		256
VP 404	442	440.5	235	242	238.5	291	289	290	284	289	286.5
YPM 1125		440			280			390			260

Specimen	Ischium Left Length	Ischium Right Length	Ischium Average Length	Ischium Left Width	Ischium Right Width	Ischium Average Width
KUVP 1300		284	284		154	154
KUVP 40002	562	540	551	263	267	265
LACM 129639a		559	559		311	311
LACM 129639b						
UNSM 55810	110.5	111	110.8	106.5	105	105.8
VP 12059			369			190
VP 404	427	440	433.5	202	204	203
YPM 1125			630			260

Table 2.2. Pectoral and pelvic girdle bivariate analysis results, including R^2 and standard deviation. Significance was determined via the slope value. A slope value was significant if it was more than two standard deviations away from 1. At a value of 1, growth would be considered isometric, values greater or less than 1 indicates positive or negative allometric growth. Significance was determined by adding and subtracting double the error of the slope to and from the slope of the regression line. When the error was included, if the slope of the line includes a value of 1, then the results were considered insignificant. Insignificant results were interpreted as possible isometric growth and significant (does not cross a value of 1 for the slope) results suggested allometric growth. * denotes statistical significance

Element Bivariate Analysis	R^2	R^2 adjusted	Equation of line	Slope value	Error on slope
Scapula Width by Length	0.9051	0.8892	y=1.213+0.7539x	0.7539*	0.0997
Scapula Width by Anteromedial Length	0.9218	0.9088	y=0.2538+0.9499x	0.9499	0.1129
Coracoid Width by Length	0.9416	0.9319	y=-0.3257+1.1413x	1.1413	0.116
Pubes Width by Length	0.9234	0.9106	y=-1.0358+1.2068x	1.2068	0.1419
Ischium Width by Length	0.9157	0.8988	y=-2.3271+1.554x	1.554*	0.2109

Appendix B: IRB letter

MARSHALL UNIVERSITY
www.marshall.edu

Office of Research Integrity

February 21, 2013

Christina Byrd
2001 6th Ave. APT 1312
Huntington, WV 25703

Dear Ms. Byrd:

This letter is in response to the submitted thesis abstract titled "Ontogenetic Variation Among Polycotylid Plesiosaurs (Sauropterygia: Plesiosauria)." After assessing the abstract it has been deemed not to be human subject research and therefore exempt from oversight of the Marshall University Institutional Review Board (IRB). The Code of Federal Regulations (45CFR46) has set forth the criteria utilized in making this determination. Since the information in this study does not involve human subjects as defined in the federal regulations it is not considered human subject research. If there are any changes to the abstract you provided then you would need to resubmit that information to the Office of Research Integrity for review and a determination.

I appreciate your willingness to submit the abstract for determination. Please feel free to contact the Office of Research Integrity if you have any questions regarding future protocols that may require IRB review.

Sincerely,

Bruce F. Day, ThD, CIP
Director
Office of Research Integrity